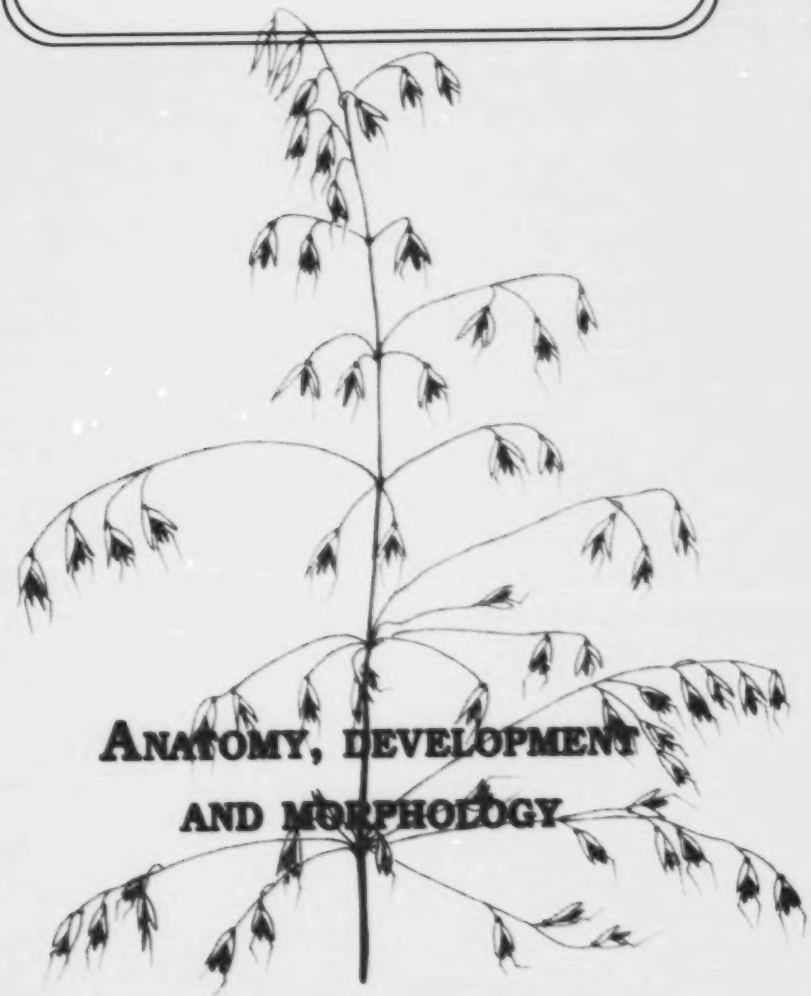
M.V.S. RAJU

THE WILD OAT INFLORESCENCE AND SEED



ANATOMY, DEVELOPMENT AND MORPHOLOGY

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CANADIAN PLAINS RESEARCH CENTER
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For David and Sylvia

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PREFACE

The wild oat (*Avena fatua* L.), a member of the Gramineae, is regarded as a noxious weed in many parts of the world. Since the time of its introduction unknowingly into North America by the early settlers, the wild oat has dispersed throughout the continent, with a major distribution in the Great Plains area causing considerable yield reductions in cultivated crops, especially the cereals (Banting 1977; Baum 1968; Sharma and Vanden Born 1978). In a recent survey, this weed was reported to be present in about 70 percent of the cultivated fields in the prairie provinces of Canada, with a mean density of 14 to 18 plants per m^2 (Thomas 1983).

A variety of control measures, both mechanical and chemical, have been applied to prevent the spread of the weed (Banting 1977; Smith 1983; Smith and Hsiao 1984). The results so far have not been encouraging (Banting 1977; Jones 1976; Simpson 1984). Genetical and physiological studies of plants in the prairies, where different herbicides are applied to control the spread of wild oats, have shown that in the agricultural areas many new genetic strains have appeared, and that some have reportedly become herbicide tolerant (Naylor 1983; Simpson 1984). The seeds (caryopses) of these different strains can be screened according to their degree of seed dormancy. However, no appropriate morphological details in distinguishing these strains are available at present.

The two important mechanisms that have made the wild oat plant a successful annual weed in the agricultural fields of the prairies are: (1) the ability of the seeds, which form the only means of propagation, to persist as dormant seeds for several years in the soil, and (2) the seeds' lack of ability to germinate uniformly once dormancy is broken (Banting 1977; Johnson 1935; Thurston 1957). This phenomenon of dormancy or delayed germinability in wild oat seeds was recognized 76 years ago by Atwood (1914), and subsequently many investigators have studied in great detail the physiological problems involved, with a view to determining the control mechanisms of dormancy and germination in

wild oats (see Bewley and Black 1978, 1982; Naylor 1983; Simpson 1978). However, there have been few extensive studies on the ways the structure and development of the wild oat seed relates to dormancy and germination. Because of the need by physiologists for such information, Agriculture Canada awarded me a special grant to carry out research for "Light microscopic studies of the structure, development and germination of the seed of *Avena fatua* L. (wild oats)."

The origin, structure and development of the wild oat seed were studied in considerable detail, both in the field and in plant-growth cabinets. The results were interesting and substantial, and this book is a product of my study. Essentially, this account is a morphological treatise described under different headings. It begins with a short review of the distribution and the taxonomic status of the wild oat. Description of the general morphology of the vegetative plant is brief as it is similar to that of the cultivated oat (Bonnett 1961). More details, however, are given with respect to the structure and development of the inflorescence. Anatomy of the spikelet and the floret is described in detail, with some unconventional morphological interpretations. Embryological details are extensive and, here again, I have presented some interpretations that are different from the generally held views. A detailed account of the origin and development of the envelopes which surround the embryo is given with the view that it will be useful in studies of seed dormancy and germination. The information dealing with the anatomy of the mature caryopsis, with all its important components, and of the embryo, with its own parts, will aid in comparative studies of different taxa of the Gramineae and, possibly, also closely related monocot families. There is also a brief account of caryopsis germination which, in many respects, has been attempted from a morphologist's point of view. Finally, the conclusions and comments section contains a general account of the interpretations of the grass inflorescence, the significance of double fertilization in seed formation in angiosperms, the probable events in the onset of dormancy and germination, and the role of embryo envelopes in caryopsis germination. Some phylogenetic problems, especially relating to grasses

and monocots, are briefly mentioned. I hope that the information presented in this book will form the basis for further investigations on wild oats.

While studying in detail the structure and development of the inflorescence and seed of wild oats, a few reinterpretations of morphological significance have been provided. The views expressed here are based on available results from my present research and previous studies. Some interpretations may be morphologically controversial or considered radical. It is left to readers to judge and to criticize the views presented in this book. Repetition of some information is apparent in a few sections, and this has been done deliberately in order to allow readers to follow the specific topic without losing the general trend.

The list of papers cited in this book is by no means exhaustive. A computer search of the literature on wild oat seeds produced more than 1400 publications on various aspects of seeds. Therefore, attempts have been made to select only a few pertinent publications. For additional references, readers may consult Rost and Lersten (1973) and Simpson (1987, 1988, 1990).

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INTRODUCTION

Cannon (1900) was the first to study the morphology of the flower and embryo of the wild oat, *Avena fatua* L. He provided some details about the ontogeny of the floral parts and the development of the embryo sac and embryo. No doubt they were considered as substantial and adequate at the time. But a re-examination suggested that some details were inaccurate, or too inadequate to be considered as basic information for other studies on wild oats. Cannon did present some statements and concepts which could be regarded as acceptable at present despite a lack of sufficient supporting evidence. For example, he suggested that the spikelets were sympodial in growth. This concept, although I agree with it, is in contradistinction to the current view of many investigators, who consider the spikelet to have monopodial growth. Besides this morphological publication, there is a more recent paper published on the structure of embryo envelopes or caryopsis covering layers (Morrison and Dushnicky 1982). They have described in detail the structure of envelopes surrounding the embryo in a mature seed with the help of scanning electron micrographs (SEM) and light microscopic illustrations. Although this information is important, developmental details of the envelopes are still lacking; neither does it aid in comparative studies of embryo envelopes in other related forms. Lately, some studies (Raju and Tom 1986; Raju et al. 1986, 1988a) have clearly shown that the embryo envelopes are indeed important in relation to caryopsis germination. These limited details suggest that there is a need for a detailed study of the origin and development of the wild oat seed and its associated structures.

CIRCUMSCRIPTION AND DISTRIBUTION

The genus *Avena* (oats), which includes both the wild and the cultivated oats, appears to have originated in the Middle and Near East, where early agriculture started. It is distributed predominantly in the northern hemisphere, but is reported to have spread to the southern hemisphere, especially in countries, such as Argentina, Chile, South Africa and Australia, where cereal crops are intensively cultivated (Baum 1977).

In North America, the term wild oats refers to three species, *Avena fatua* L. (common wild oats), *A. sterilis* L. (wild red or animated oats), and *A. barbata* Pott ex Link (slender oats), whose chromosome numbers are 2n=42, 2n=42 and 2n=28 respectively (Baum 1977; Martin et al. 1976).

Avena barbata occurs predominantly in waste areas in Britain, southern Europe and northern Africa, with a sparse distribution toward the eastern parts of the world (Baum 1977). It has also been found in agricultural areas of Australia and South America (Baum 1977). In North America, it is abundantly distributed in the western United States, especially in California, where it forms an important range grass (Martin et al. 1976).

Avena sterilis is infrequently distributed in cultivated and uncultivated areas of North America (Martin et al. 1976). On the other hand, it is common in different habitats, both cultivated and uncultivated areas, in Britain, and extending into Asia Minor, through the Mediterranean and North Africa (Baum 1977; Thurston 1982).

Avena fatua, the most common of the three species, is widely distributed in many parts of the warm temperate areas of the world (Baum 1977). In North America, it occurs in most agricultural areas, especially in the prairies of the Great Northern Plains of the United States and Canada (Martin et al. 1976; Sharma and Vanden Born 1978).

DESCRIPTION AND GENETIC POLYMORPHISM

In a taxonomic monograph of the genus *Avena*, Baum (1977) has given a vivid description of the three species of wild oats, *Avena barbata*, *A. sterilis* and *A. fatua*. Of the three species, which are commonly regarded as wild oats, *A. barbata* can be delineated easily from the other two species. However, *A. sterilis* and *A. fatua* have such overlapping characteristics that it is difficult to separate them taxonomically. Therefore, like many investigators (Baum 1977; Looman and Best 1979; Packer 1983; Sharma et al. 1978), I have assumed that the species occurring in the Canadian prairies is, in fact, *A. fatua*. I have found that one distinct difference between the wild oat, *A. fatua*, and the cultivated oat, *A. sativa*, is that the former has a functional awn in a spikelet, which is capable of twisting and untwisting, and the latter does not.

Most weed species are known to be polymorphic (Harper 1977). Consequently, the taxonomic delineation of species becomes difficult. Therefore, detailed studies need to be conducted both for a better understanding of the variations and also for delimiting species (McNeill 1982).

Significant genetical and physiological studies have been carried out on *Avena fatua* seed dormancy and germination (Naylor 1983). The results of these studies have shown that this species exhibits tremendous morphological variations. Although many of these variations have not been recorded, they have been interpreted to be due to genetic effects (Jain and Marshall 1967). Basing his conclusions on certain morphological features, Baum (1977) has recognized many variants of *Avena fatua*. Nonetheless, taxonomic separation of the local species remains difficult. In the agricultural prairies of Canada, variations in the species, especially in seed dormancy, have been recognized and studied (Jana and Naylor, 1988; Jana et al. 1979; Naylor and Jana, 1976), thus

aiding in the isolation of many genetic strains. These variations in seeds collected from natural populations growing in different sites, have led researchers to conclude that the observed variations are, in fact, adaptations to local agronomic practices (Jana and Naylor 1980; Naylor 1983). A similar but more restricted concept has been developed, namely that some variations are also due to the effects of a variety of herbicides (Jacobsohn and Anderson 1972).

MATERIALS AND METHODS

Six genetic lines of *Avena fatua* L. were used in my study. These lines, which were earlier isolated from natural populations of wild oats by the late Prof. J.M. Naylor of the University of Saskatchewan, are being maintained at the Agriculture Canada Regina Research Station. These lines are graded according to the degree of seed dormancy, and they can be arranged in an increasing sequence — SH 430–CS 40–SH 319–AN 474–AN 51–IDAHO–MON 73, the last being the most dormant. Because of the structurally recalcitrant nature of plant material, especially the caryopses (seeds), the plant parts were carefully selected and processed to suit the aspect of investigation. Most information presented in this book, especially on seed structure and embryology, comes from CS 40 (nondormant) and/or AN 51 (dormant) strains.

Observations were made on plants of different lines raised in experimental plots at the Agriculture Canada Regina Research Station. Some critical observations were also made on plants of selected strains (CS 40 and AN 51) raised in the environment-controlled growth cabinets at the University of Regina. In the growth cabinets, constant environmental conditions were maintained with a 16 h photoperiod, a night/day temperature of $22^{\circ} \pm 2^{\circ}$ C and a relative humidity of 50-60 percent. The light intensity in the growth cabinets was 300 μ E.$m^{-2}S^{-1}$. All plants were grown in garden soil with sand and perlite.

Histological and histochemical studies were made on suitable plant materials collected from plants in the field and also in the growth chambers. Conventional methods of collecting, fixing, and processing were followed (Berlyn and Miksche 1976; Jensen 1962; Johansen 1940). Plant materials were fixed in formalin-acetic acid-ethanol (FAA) and processed for paraffin embedding by using graded ethanol—xylene or ethanol—1-butanol series (Jensen 1962;

Johansen 1940). The paraffin-embedded materials were microtomed to obtain 8-10 μm thick sections for staining and microscopic examination.

In most instances the sections were stained by following the Delafield-Hematoxylin procedure with or without counterstain (Johansen 1940). Some sections were counterstained with erythrosin in clove oil. Schiff's reagent was used in some cases by following the PAS or Feulgen method (Jensen 1962). Safranin-Fast Green procedure was also followed to stain some sections (Johansen 1940).

Some specific plant materials were carefully cleared in 0.5% aqueous NaOH for 8–24 h at 40°C to separate or isolate different tissues, or to determine the course of vasculature. They were washed well in distilled water, then aqueous 0.5% of basic fuchsin, or of crystal violet, was used to stain their vascular tissues. My study used both fresh and preserved plant specimens to obtain the desired results. Iodine potassium iodide solution (1% aqueous) was used to identify starch grains in cells in fresh materials.

GENERAL MORPHOLOGY

In the field, wild oat seeds (caryopses) germinate very early in the spring and within a few days a well-developed seedling is established. A 5-day-old seedling can have a root system with a measured root length of 87 cm (Pavlychenko and Harrington 1934). When some deeply buried seeds germinate, the shoot is pushed to the surface by the tremendous elongation of mesocotyl of the seedling (Sharma et al. 1976; Thurston 1961).

The seedling can mature in about 8–9 weeks after germination by producing a terminal panicle, which produces mature caryopses or seeds about 5–6 weeks later. Each shoot or axis produces 6–7 vegetative leaves before the emergence of the panicle. Meanwhile, the main axis, especially in its proximal parts, will have produced many tillers or branches, which, like the main axis, may bear terminal panicles. The shoots, main or tillers, contain nodes and internodes as in other grasses. Each internode is enveloped by the leaf sheath arising in the subjacent node. The nodes in the proximal regions of the axis produce adventitious roots.

Table 1 shows some morphological features in different genetic lines of wild oats. Among plants grown in experimental plots, the dormant lines show a tendency to produce more tillers and, consequently, they have more panicles per plant than the nondormant lines. There is no regular pattern to relate other morphological features to the dormancy characteristics of the wild oat lines. As the number of nodes in the panicles is similar, the differences in the number of panicles per plant and spikelets per panicle may be attributed respectively to the degree of tillering of the plant and the branching of the panicle (Table 1). More detailed study is needed in this regard.

INFLORESCENCE

The inflorescence in wild oats is a panicle, a term commonly applied to the inflorescence of grasses. It is rather difficult to define, although Lawrence (1951) considers it as an indeterminate branching raceme which in the present context seems to be inappropriate. Bonnett (1961) has described in detail the panicle for cultivated oats (*Avena sativa*). The mature panicle in wild oats has a determinate axis consisting of 6–10 nodes on the main rachis of the main shoot, and of 5–8 nodes on the rachis of tiller branches (Figs. 1,2; Table 1). Ordinarily, the basal-most node of the inflorescence contains the largest number of branches, which may show first and second degree branches each terminating in a spikelet. The branches decrease in number in the nodes toward the distal end of the inflorescence. Each node on the axis has a highly reduced scaly leaf which subtends a cluster of branches. The arrangement of branches at nodes on the panicle axis appears two-ranked, similar to the distichous arrangement of vegetative leaves on the shoot; however, they do show an overall spiral arrangement on the panicle axis.

In wild oats, as in many grasses, the basic units of a panicle are the spikelets, each of which has been considered a modified shoot (Bonnett 1961). The number of spikelets per panicle varies depending on the genetic strain of wild oat, and whether the panicle is on the main axis or on the tiller (Table 1). Each spikelet contains a variable number of florets which may range from 2–4 or 5. In most instances, the first two, which are often designated as primary and secondary, florets show normal grass floral structure and eventually produce viable seeds.

Development of the panicle

In about 19–20 days after caryopsis germination, and following the initiation of the last leaf primordium (flag leaf), the vegetative shoot apical meristem becomes transformed

into a reproductive or panicle meristem. The most distal part of the transformed meristem eventually differentiates into the first spikelet initial (Figs. 3–5) similar to that of the cultivated oat (Bonnett 1961). The flag-leaf primordium continues to grow enclosing the transformed panicle initial. Meanwhile, additional branches appear laterally on the panicle-initial axis, in which the nodes become differentiated (Figs. 6–12). The regions between nodes, the internodes, begin to elongate concomitantly with the differentiation of spikelets on these branches and, consequently, the nodes and internodes on the main or central axis of the panicle become distinct (Fig. 12).

The tips of the lateral branches are the first to differentiate into spikelet initials (Figs. 4, 5). More spikelet primordia appear on the panicle axis, especially at the proximal nodes (Figs. 8, 10). Such primordia are the last to differentiate into spikelet primordia.

In a well differentiated panicle, which is still enclosed in the flag-leaf sheath (Fig. 10), branches can be isolated from the nodes on the panicle axis (Fig. 8). In Fig. 9 these branch primordia are sequentially arranged from the basal-most to the distal-most parts of the panicle. It is clear that the most distally placed spikelets (Fig. 9d) are better differentiated and more mature than the proximally situated spikelets (Fig. 9a) in which the glumes and the other floral parts are well developed.

Thus, in the entire panicle both differentiation and maturation of spikelets proceed basipetally from the distal end to the proximal end of the panicle axis or rachis. A similar pattern of maturation of spikelets occurs also in each of the lateral branches of the panicle. However, some initials, which appear much later, usually contain single spikelets whether they arise on well-developed branches or are formed in the nodes independently of the branches, contain usually single spikelets (Figs. 1, 2). Even when there are many spikelets, the most distal one matures first. In the development of the wild oat several sequential stages can be recognized which together take considerable time. After the transformation of the shoot apex from vegetative to reproductive status, the complete differentiation of the distal

spikelets of both the main axis, and the lateral branches of the panicle, is completed in 6–7 days. The differentiation of spikelets in the entire panicle, before emerging through the flag-leaf sheath, takes about 13–18 days after the vegetative shoot apex has changed to the panicle apex (Table 5).

The histological details regarding the origin of branches in the panicle are similar to those described for the cultivated oat (Bonnett 1961).

Development of the spikelet

In wild oats, as in other grasses, the spikelet forms the basic unit of an inflorescence or a panicle. The spikelet itself can be considered as an inflorescence containing one to many florets (Figs. 13, 14, 18). Irrespective of the number of florets within, the spikelet is enclosed by two leafy envelopes, the glumes, the first formed outer glume, or glume one, and the younger inner glume, or glume two. The inner, or second glume, contains in its axil a small axis called rachilla one (Fig. 13, 14). Each floret in wild oats contains floral parts, such as lemma, palea, lodicules, stamens and pistil.

A comparative study of seven different strains of wild oats shows that the number of florets in each spikelet may vary from 2–5. In most instances, the first two florets are normal with the usual floral parts. If the number of florets exceeds two, the others show different degrees of abnormalities with respect to the development of floral parts, which appear as rudimentary structures. In some strains (AN 51), the third floret also may develop normally, eventually producing a viable seed, which, however, remains smaller than those of the first (primary) or the second (secondary) florets.

It is generally considered that a spikelet of a grass consists of a set of overlapping rachillae to form a central or spikelet axis. This axis, bearing laterally placed florets, is subtended by a pair of glumes, which envelope the florets. On the spikelet axis are the distichously arranged bracts or lemmae in whose axils are short axes. Each axis bears appendages, from base upwards, such as palea, lodicules, and stamens. The axis terminates in an ovary. Some of these appendages and their morphology have been described, discussed, and interpreted variously (see Clifford 1986). In wild oats, the

spikelet is similar to the cultivated oat (Bonnett 1961) with respect to the placement of the florets on the spikelet axis (Figs. 14, 18, 19). Some critical observations and histological studies indicate that the spikelet is, in fact, determinate and it can be called a "cymelet." However, the term "spikelet" is so deeply entrenched in the literature that it is difficult to change to any other terminology at present, and I have used it in this book.

In about 3–5 days after the changeover of the shoot apex from vegetative to reproductive state, its most distal part becomes differentiated into a spikelet (Figs. 13, 16). Evidences of organogenesis in such a spikelet suggest that the first and second glumes are differentiated first and, following them, are the florets. The floret differentiation on the spikelet axis is acropetal: the earliest formed floret is in the most proximal end and the most recently formed one is distally placed. Such an acropetal differentiation of florets in a spikelet is a reverse of what is observed in a panicle where the spikelets are differentiated basipetally on the panicle axis or rachis (Figs. 10–12).

The appendages of a floret are initiated in sequence on the spikelet axis: *lemma—palea—lodicules—stamens—pistil*; the development of these organs follows the same sequence. It is important to know at this stage whether the actual position of the florets in relation to the spikelet axis, is lateral or terminal. Sections of young panicles at different stages of development show that the florets in a spikelet are indeed terminal, rather than lateral, as in racemes or spikes (Figs. 14, 18, 55). Consequently, the rachilla, which distally supports the floret, is a lateral organ, and it can be considered as an axillary shoot (Figs. 13, 16–18). In a young spikelet primordium, the rachilla, which distally supports a floret, is a lateral shoot situated in the axil of a subtending lateral appendage, the bract (Figs. 13, 16). The presence of a bract in sections of young spikelets is quite obvious (Fig. 13). However, in later stages of spikelet development, when considerable elongation of the spikelet axis has taken place, the bract becomes inconspicuous, and often lost. It is also difficult to consider the bract as a part of the lemma, which is situated on the opposite side of the bract (Figs. 13, 16, 17).

The reason for its poor development, or for its disappearance in later stages of spikelet development, is probably its lack of vascular development. The disappearance or modification of certain floral parts during development is not uncommon in angiospermous flowers (Puri 1951).

In a mature spikelet, the axis between the base of the floret and the glumes is interpreted as the first rachilla, terminating in the first floret (Figs. 13–18). There is a short region, or stalk, lying between the first rachilla and the lemma base (first floret base), and this is interpreted as the pedicel of the first floret (Figs. 18, 55). This short pedicel is an important region of the floret where anatomical changes occur during the formation of vascular traces which pass into the second rachilla and to other parts of the first floret (Fig. 18). Similarly, the second rachilla, arising as an axillary branch on the first pedicel, terminates in the second floret, and so on with others (Figs. 14, 18). In addition, an abscission zone is laid down between the pedicel of a floret and the summit of the rachilla, and as a result the diaspores, that are formed in the spikelet, are disarticulated. Each diaspore unit is made up of a pedicellate floret-enclosed caryopsis and its associated rachilla. The first rachilla is always the distal part of the peduncle of the entire spikelet in wild oats. Therefore, the first floret will comprise the second rachilla, the second floret will have the third rachilla, and so on (Figs. 14, 18). In a mature spikelet, the floret-enclosed caryopsis, with its persistent floral parts and the rachilla, is the diaspore, caryopsis, or seed. In wild oats, several categories of caryopses, such as primary, secondary, tertiary, etc., can be distinguished. Such diaspores, which drop off the parent plant, can be identified by the length of the rachis or rachilla associated with each of the categories (Table 2). The primary caryopsis has a shorter rachis than the secondary. The longest rachilla or rachis is present in the tertiary caryopsis.

Vascular anatomy of the spikelet

Each spikelet of wild oats comprises two or more florets and, therefore, it is an inflorescence. The stalk of the inflorescence is then a "peduncle" instead of a "pedicel," a

term applied to the stalk of an individual floret or flower (Fig. 55). Immediately below the region of insertion of glumes (inner and outer) the peduncle is radially enlarged in contrast to its more proximal part, which is more or less a flattened or dorsiventral structure (Fig. 55). The peduncle extends beyond the level of insertion of glumes and forms a short radial axis designated as the first rachilla of the spikelet (Fig. 55). The first or the primary floret is situated on this first rachilla (Figs. 13–18, 55). Arising from the base of the floret is the second rachilla which, in turn, terminates in the second floret (Figs. 18, 55).

The proximal part of the peduncle contains a row of vascular bundles, about four in number, giving also a dorsiventral morphology to that part of the peduncle (Figs. 27, 28). These bundles, as they proceed toward the distal end, divide or branch, producing more vascular bundles, which arrange themselves more or less in a ring (Figs. 29–32). Subsequently, some of these peripherally placed bundles diverge to become the vascular bundles of the first or outer glume (Fig. 33, 34). The bundles within the glume, especially the outer ones, may divide to form 9 to 11 bundles. Similarly, the bundles of the axis situated opposite to the first glume diverge to the periphery to form the bundles of the second or inner glume (Figs. 35–37). The remaining fewer bundles, two or three, become the bundles of the first rachilla (Figs. 35, 36). Most commonly, the two bundles seen in the rachilla (Figs. 34–37) arrange themselves in such a way that they form the adaxial and abaxial bundles of the first rachilla (Figs. 36, 38). The two collateral vascular bundles, adaxial and abaxial, have inverted orientation of xylem and phloem as in a radial stem; the xylem of one bundle faces the xylem of the opposite bundle. The adaxial bundle is usually more massive, especially toward the distal end of the rachilla; the abaxial bundle continues into the second rachilla above without producing branches to become the outer bundle of the rachis or rachilla. The adaxial bundle, on the other hand, divides to form several branches or bundles (Figs. 38–42, 55). The earliest branch, which produces a branch connecting the outer rachis bundle, continues as an unbranched bundle lying parallel to the

outer rachis bundle (Fig. 55); it extends further into the second rachis to form its inner bundle (Fig. 42–50, 55). The traces, which move into the second rachilla, are the first to emerge from a group of bundles situated in the region just above the first rachilla and below the first floret (Fig. 42). This highly diminutive region is designated here as equivalent to a pedicel, and it is here that considerable branching of the adaxial bundle occurs (Figs. 42, 55). After producing the second rachis trace the adaxial bundle becomes the floral bundle supplying traces to the first floret in the spikelet (Fig. 55). The floral bundle divides to produce many bundles of the axis which eventually provide traces to the floral appendages (Figs. 45–55).

Floret anatomy

After the traces of the second rachilla have departed from the pedicel of the first floret, the lemma traces opposite the traces of the second rachilla emerge and eventually become the bundles of the lemma of the first floret (Figs. 19, 55). At about the same level, one or two sections higher, and opposite to the lemma, two traces appear leading to the two keels of the palea (Figs. 19–23, 43–45, 55). Serial cross sections indicate that the palea arises as two distinct primordia, one on either side of the second rachilla. However, in the later stages of development they undergo lateral cohesion to form a single bi-keeled palea situated opposite to the lemma (Figs. 23–26, 44, 45). Immediately following the departure of the palea traces, two independent traces of the lodicules appear opposite the palea (Figs. 22, 23, 46). Each lodicule trace lies between the median bundle of the lemma and the single keel bundle of the palea. If there were a third lodicule in the floret of wild oat, then the bundle of this lodicule would lie between the two keels of the palea. In fact, the initiation of a ventral lodicule, which arises shortly after the palea, has been described for *Stipa tortilis* and *Oryzopsis miliacea* (Maze et al. 1971), although the morphological interpretation of it is rather different. The remaining stamen-carpellary bundle divides to form a few bundles at a higher level, resulting in three stamen traces, two lying opposite the median bundles of the palea, and the third

opposite the median bundle of the lemma, alternating with the two anterior lodicules (Figs. 24–26, 48). This arrangement indicates that the stamens together form a single inner whorl. The two anterior lodicules could be considered to belong to an outer whorl, although its posterior one is missing in the floret.

The remaining vasculature in the middle of the floret axis is that of the carpel, which also supplies the ovule (Figs. 25, 26). Higher up in the ovary wall the carpellary bundle branches giving traces to two styles. This pattern of vascular relationship between the carpellary bundle and styles (stigmas) is similar to the vegetative scutellar and coleoptilar bundles in the mature embryo (see Fig. 191H–M); the bundle of the scutellum branches to produce two coleoptilar traces which become bundles of the coleoptile at the coleoptile node.

At about the stage when the floret traces and bundles are being organized, especially in the pedicel of the floret (Figs. 42–44, 55), the bundles of the second rachis become conspicuous and appear as two inverted bundles (Fig. 45, 55). The outer (abaxial) bundle becomes the adaxial bundle or outer rachis bundle, behaves like the adaxial bundle of the first rachis, and ultimately becomes the floret bundle. The inner (abaxial) bundle in the second rachis remains unbranched and enters finally into the third rachis to become the outer rachis bundle (Fig. 55).

The origin and departure of the rachilla bundles earlier than the floret bundle and its branches, and the presence of two inverted collateral bundles in the rachis, suggest that the rachis, although attached to the base of the caryopsis (floret-enclosed-caryopsis), is a cauline structure, and not a part or an appendage of the floret. The rachis is a radial organ (shoot) representing a lateral (axillary) shoot. The outer bundle of the rachis (rachilla) becomes thicker toward its distal end where it is associated with the traces of appendages of the next (second) distal floret (Figs. 18, 55). The entire pattern of vascular differentiation seen in the rachilla (rachis) and the floret bundle is repeated as long as viable or complete florets are present distally. However, after the development of the third rachilla in wild oats, subsequent

rachillae usually show morphological and anatomical abnormalities during development and differentiation. Consequently, interpretation of the anatomy or morphology of the florets and their appendages becomes difficult.

The entire inflorescence of wild oats is determinate (Raju and Ramaswamy 1983; Raju et al. 1985), and the units of the inflorescence, the spikelets, are determinate as well. Anatomically, the panicle of wild oats is simple, although it appears complex because of the large amount of branching and some modification, by elaboration or suppression, of certain vegetative and floral parts of the inflorescence. The occurrence of these features are not unusual in other grass inflorescences (Gould 1968; Clifford 1986). The branching pattern of the entire inflorescence is laid down long before its emergence through the flag-leaf sheath. After its emergence, the branching pattern seen in a mature inflorescence is achieved by elongation only (Figs. 1, 2).

Panicle and spikelet—an interpretation

Anatomical and developmental studies of the panicle and spikelet of wild oats suggest several interesting features. The shoot apical meristem differentiates into a segmented axis consisting of nodes and very short internodes (Fig. 12). The branch primordia are initiated in the nodes, somewhat distichously. At about this stage, the tip of the main axis of the panicle differentiates the first spikelet. Following this the nodal branches begin to elongate, and the tips of the branches become modified into spikelets as in the main panicle axis. Thus, both in the main axis and in the branches of the panicle, the first spikelet is formed at the tip and the other spikelets are differentiated subsequently on the axis, indicating a basipetal pattern of differentiation of spikelets. In individual spikelets, however, the florets are initiated acropetally, the basal ones differentiating earlier than the more distally placed florets.

Terms such as "panicle" and "spikelet" are common in the literature on grass morphology. In grasses, the inflorescences are neither panicles nor spikelets (Gould 1968). My study supports this view. In wild oats the panicle and the spikelet are determinate inflorescences of the cymose type. The

spikelets, both in the main axis and in the branches, mature in the distal region earlier than in the more proximal regions.

The spikelet of wild oats is an inflorescence consisting of two to many florets. According to the generally accepted view, the sessile florets are arranged on the axis in an acropetal fashion. The first formed florets are situated in the proximal parts and mature earlier than those in the distal region on the spikelet axis, indicating an acropetal pattern of maturity. The spikelet, according to this interpretation, may be called a spicate inflorescence. However, the results of my anatomical study suggest a different interpretation. Each floret is terminal situated at the distal end of the rachilla, which, in fact, is considered here as a branch closely associated with the mature caryopsis. Therefore, the growth of the spikelet is sympodial, an interpretation similar to Cannon's proposal (1900). The spikelet of the wild oat then is not a "spike," but a cyme. The basic unit of the panicle of the wild oat is more appropriately a scorpioid "cymelet," rather than a "spikelet".

In grass systematics and morphology, a variety of definitions have been given in regard to the floret and its appendages (Arber 1934; Barnard 1964; Clifford 1986; Kam 1974). Barring some complicated interpretations, most taxonomists and morphologists consider that the grass floret is monochlamydeous (Arber 1934; Bonnett 1961; Clifford 1986; Estes et al. 1982; Guédès and Dupuy 1976; Troll 1957). The acceptance of this interpretation is based on the view that the lodicules would represent the perianth lobes. As in other grasses, the floret of wild oats consists of appendages, such as lemma, palea, lodicules, stamens and pistil. My investigations support the view that the floret is monochlamydeous. However, the interpretations provided in support of this view are somewhat different.

Each floret is situated at the distal end of a rachilla. In wild oats, the mature floret (floret-enclosed caryopsis) becomes separated from the rachilla by the development of an abscission zone between these two organs. What is ordinarily referred to as the dislodged "caryopsis", is a dried mature caryopsis, covered by hull or husk, which represents the dried parts of the floret. Therefore, the "caryopsis" is more appropriately termed a "floret-enclosed-caryopsis" (Raju

and Ramaswamy 1983). Several florets of this kind still remain attached in the inflorescence, and are together covered by the inner and outer glumes, as in many other grasses when the entire unit is referred to as the "spikelet."

The floret appendages in grasses show different sequences of their origin (Clifford 1986). In wild oats, as in cultivated oats (Bonnett 1961), the sequence of initiation of floral appendages is *lemma—palea—lodicules—stamens—pistil*. The floret axis, including the stalk or pedicel, of the floret between the lemma and the rachilla is so short (Bonnett 1961) that the correct sequence of initiation of lateral appendages becomes difficult to determine; it is also difficult to discover if the appendages are arranged spirally or in whorls.

The floret bundle is organized immediately after the rachilla traces have departed from the floral axis in the pedicel. The lemma and palea traces in a floret arise at about the same level on the floral axis, and in this volume they are interpreted as belonging to one whorl. The commonly accepted view is that the lemma is an appendage subtending the floret and, therefore, that it is a bract (Arber 1934; Clifford 1986; Kam 1974). The palea in its ontogeny arises as two distinct lobes which, in later stages of development, fuse laterally to form a single structure. In some instances, however, the bifid nature is retained in mature palea, and this feature results in palea being regarded as bracteoles. In my study, the two keels of palea and the lemma are together interpreted as belonging to a single perianth whorl.

The morphologically controversial appendages of a grass floret have been the lodicules (Clifford 1986; Kam 1974). They are generally considered as representing modified perianth lobes which are more of a foliar nature (Arber 1934; Barnard 1955, 1957; Cronquist 1981; Guédès and Dupuy 1976). On the other hand, the same lodicules, based on ontogenetic studies, have been regarded as cauline structures (Bonnett 1961; Maze et al. 1971; Mehlenbacher 1970). Their cauline nature has also been recognized by specifically considering them as staminodes (Turpin 1819).

The lodicules in wild oats, as in other grasses, serve primarily the function of anthesis. Immediately after anthesis

they burst, losing their morphological integrity and presumably also the ability to regenerate (Raju et al. 1985). It is not possible to find well-differentiated tracheidal and sieve elements in such lodicules except at their bases where lodicular traces enter into them. However, partly differentiated tracheidal and sieve elements are common in the swollen bases of lodicules at the time of anthesis. In instances where the lodicules last longer without showing much physical damage, the occurrence of both tracheidal and sieve elements is obvious (Pizzolato 1980a,b, 1983). There may be cases where ambient conditions might prevail for the early differentiation of xylem and phloem within the lodicules. The occurrence of rudimentary stomates or pores in lodicules is not uncommon (Pizzolato 1980b).

The stamens in trimerous flowers appear immediately after the inner perianth lobes (Lawrence 1951). If these stamens are arranged in a whorl, they usually alternate with the inner perianth lobes. The two anterior grass lodicules together with a posterior lodicule, which is absent in the wild oat floret, can be regarded as a trimerous whorl of modified stamens alternating with the lemma and the two keels of the palea. The three functional, or true, stamens of the inner whorl of a wild oat floret, alternate with the outer lodicules. Such an arrangement of two or more whorls of stamens, each alternating with the other, is not uncommon in angiosperm flowers (Lawrence 1951). In some groups, such as the Primulales, the stamens are antipetalous in flowers (Lawrence 1951). In such instances, anatomical investigations have shown that the outer whorl of stamens, alternating with the petals, is suppressed or modified into glands, staminodes, etc. (Lawrence 1951; Puri 1951; Raju 1953). Based on such interpretations, it is not unreasonable to consider the whorl of lodicules as modified stamens (see Clifford 1986; Turpin 1819). Despite functional differences, there are some structural similarities between lodicules and stamens. The occurrence of a single vascular trace at the base of these two organs, the reduced vasculature in both, the arrangement of both in whorls, one alternating with the other, and the occasional development of rudimentary

stomates, or pores on them, provide evidence of morphological closeness of lodicules and stamens.

The grass pistil appears to be of the pseudomonomerous type (Eames 1961) consisting of a single locule with a single ovule. The simplicity of the pistil in wild oats, and possibly in other grasses, may be derived from a primitive trimerous condition. This concept agrees with Philipson's (1985), who considers the tricarpellary condition as primitive. Comparative morphological, anatomical, and developmental studies, comprising many genera of grasses are needed to interpret the simple nature of the pistil in grasses. Two of the three carpels of the ancestral form probably suffered a developmental degeneration, leaving behind one functional carpel in the present form. An instance of this kind is seen in *Euphorbia esula* where 3–6 carpels appear early in ontogeny (Raju, unpublished data). During development, however, only three carpels survive to form a tricarpellary pistil in this species of the Euphorbiaceae; the other carpels disappear, leaving behind no recognizable trace in a mature pistil. Occasionally, it is possible to find in wild plants 4–6 normally developed carpels as an abnormality in the pistils of this species.

I suggest, therefore, that the florets of wild oats with trimerous floral parts are similar to other monocotyledonous flowers. The floret can be regarded as monochlamydeous with the outermost perianth whorl comprising the lemma and two keels of the palea. The stamens are arranged in two whorls of three each, the inner whorl being functional. The outer whorl contains modified stamens or lodicules alternating with the perianth lobes; the posterior unit in this whorl is absent. The pistil with a single ovule may be regarded as pseudomonomerous (Eames 1961), the ancestral form being presumably trimerous (Cronquist 1981; Dahlgren and Clifford 1982; Philipson 1985).

FLORET AND ITS PARTS

The panicle, which is the inflorescence of a grass, contains many units called spikelets. Each spikelet, in turn, is also an inflorescence consisting of flowers. In grasses, these flowers are called florets. The ontogeny, anatomy, and morphology of the florets and their associated parts in spikelets have been studied extensively (Cannon 1900; Kam 1974; Maze and Scagel 1982; Maze et al. 1971; Sattler 1973; Sharman 1960a,b). It is generally believed that the structure and morphology of the florets and their parts are quite uniform, at least in the investigated taxa. Some details are still not clear and are being debated (Clifford 1986; Kam 1974). Some morphological work was originally carried out on *Avena fatua* (wild oats) by Cannon (1900). No major investigations have been conducted on the morphology of this taxon since then. This chapter presents the current status of the morphology of the floral parts.

Glumes

In each spikelet of wild oats there are two glumes, the outer and the inner, which have been designated as the first and the second glumes respectively (Figs. 14, 16–18). Morphologically, they are regarded as equivalent to vegetative leaves, and are arranged distichously at the distal end of the peduncle of the spikelet (Fig. 18). These glumes are anatomically similar to those described for *Avena sativa* (cultivated oats) by Bonnett (1961). They are often called empty glumes, as they are lateral organs on an axis and contain no axillary appendages. My study also reports the first glume as being empty. However, the second, or inner, glume contains a short axillary shoot or rachilla. Given their position on the peduncle of the spikelet, these glumes can be interpreted as bracts. The first rachilla in the axil of the second glume terminates in a flower. The first glume, which

does not have a branch in its axil, may have some evolutionary significance, but I will not discuss that now.

Rachilla

The number of florets in a grass spikelet may vary from one to many (Arber 1934). The florets, according to general description, are borne on an articulated axis, the rachis. Each rachis is made up of several units separated in mature spikelets by a characteristic abscission zone, and each of these units is called a "rachilla" (Figs. 14, 18, 55). Each rachilla is intimately associated with a caryopsis, as well as the other persistent dry floral parts which surround the caryopsis. In most grasses, the rachilla appears as a flattened structure and contains two antero-posteriorly placed collateral bundles (Figs. 21–26); the bundles are inverted to suggest that the entire organ is fundamentally radial. It is an antero-posteriorly compressed stem axis which I have interpreted as an axillary shoot. In many grasses, only two vascular bundles or strands are found in the entire rachilla. However, in a few grasses, the rachilla at its distal end may contain three bundles, as in *Andropogan gerardii* (Maze 1977). In *Avena fatua* the rachilla always contains two bundles of unequal thickness, the posterior always being smaller or narrower (Figs. 49, 50, 55). Anatomically, the vascular traces of the rachilla originate from the axial stelar strands as do those of axillary buds (Figs. 41–43). The rachilla strands arise before the differentiation of lemma traces, and, therefore, the lemma is interpreted to have a more recent organogeny than the rachilla. The rachilla is morphologically an axillary shoot which is somewhat an antero-posteriorly compressed organ (Figs. 14, 23–26, 50).

In some taxa, such as *Stipa*, *Anthoxanthum*, *Erhartia*, etc., the rachilla terminates in a floret or pistil (Barnard 1957; Sharman 1960a). In wild oats, the rachilla ends distally in a floret, indicating sympodial branching in the spikelet, a feature already pointed out by Cannon (1900).

Lemma and awn

In wild oats and many other grasses, a part of the leafy appendage, the lemma, is modified to form an elongated

hygroscopic structure known as the awn (Figs. 51, 52). Some awns, including those of wild oats, have the ability to twist and untwist on their own axis (Raju 1984), while the other rudimentary awns, such as those of cultivated oats, have lost this ability (Bonnett 1961).

The lemma is a leaf-like organ similar to the glume, and encloses all the other floral parts, as in cultivated oats (Bonnett 1961). The origin and development of the lemma and awn are similar to those in other grass taxa (Bonnett 1961; Kam 1974; Maze et al. 1971; Mehlenbacher 1970). In later stages of development of the floret, especially after fertilization, the abaxial base of the lemma becomes asymmetrically stretched so that the adaxial base of the lemma is lifted up and the abaxial side is lowered. Consequently, the abaxial part appears swollen due to some histological proliferation, and this modified part is commonly referred to as "callus" in the literature. However, most of the asymmetrical growth is brought about by cell elongation on the abaxial side of the base of the lemma (Figs. 55, 182–185). Similarly, in the rachilla subtending the floret, there occurs considerable longitudinal growth due to cell elongation. The cells elongate more on the abaxial side (toward the adaxial side of the floret) of the rachilla (Figs. 180–184). As a result of all these changes, the abscission zone, which was somewhat transversely oriented in the young spikelet, between the base of the lemma and the subjacent rachilla, becomes obliquely oriented in the old spikelet (Figs. 17, 18, 182, 183).

The lemma in *Avena fatua* contains about 7 vascular strands. During development, the mid-part of the linear lemma, along with its vein, becomes separated from the lemma to become a radial appendage, the awn. The single mid-vein of the lemma completely supplies the awn, which remains as a part of the lemma (Figs. 51, 52).

The basal two to three florets in a spikelet bear the awns. In the early stages of development, before gametic fertilization, the awn is straight, consisting of two parts, a basal brownish dorsiventral part and a distal green subulate part. The lateral grooves in both parts contain chlorenchyma which is associated with many stomates (Raju 1984). The shorter basal part, which is capable of twisting and

untwisting, is made up of a narrow abaxial ridge and a wide adaxial ridge, and between the ridges lie the lateral longitudinal furrows (Raju 1984). The ridges extend into the longer distal subulate awl. The stomates associated with the chlorenchyma in the longitudinal furrows contain reniform dicot-like guard cells (Raju 1984).

In later stages of caryopsis maturity, the entire straight awn gradually loses water and becomes geniculate, with the awl placed distally at right angles to the longitudinal awn axis (Raju 1984). The mature awn (basal part of the whole awn) remains twisted. In the presence of moisture, it can untwist and revert to the twisted state on desiccation. The awl, which forms the distal part of the basal awn, shows a radial rotation and often acts as a lever or brace. It does not have the ability to twist or untwist on its own axis.

Functionally, the awn is a very important photosynthetic organ, whose presence is known to increase the kernel weight in crop plants (Grundbacher 1963; McDonough and Gauch 1959; Sagromsky 1954). In addition, the awn, with its awl acting as a lever, can help in dislodging the ripe caryopsis from the spikelet (Raju and Ramaswamy 1983). It can untwist in the presence of water, causing the lemma enveloping the caryopsis to turn in the opposite direction. As a result, the entire floret-enclosed-caryopsis gets detached from the subjacent rachilla (Raju and Barton 1984), and because this mechanism causes the florets to be dislodged from spikelets in wild oats, the mature inflorescence or panicle contains only dried persistent glumes enclosing the small persistent first rachilla. The mechanisms of twisting, untwisting, and dislodging of the floret-enclosed-caryopsis have been described for *Avena fatua* (Raju 1984; Raju and Barton 1984; Raju and Ramaswamy 1983; Yeung et al. 1987). The awns of grasses are also implicated in the burial of floret-enclosed-caryopsis in soil (Darwin 1876; Peart 1979; Stinson and Peterson 1979).

Awns in grasses vary considerably in their structure and morphology and may be significant in taxonomy (Arber 1934; Clifford 1986). One of the important differences between the wild and the cultivated oats is the presence of functional awns in the former and their absence in the latter.

The lemma is an appendage of the floral axis and situated in the anterior part of the floret. In my study, it is regarded as one of the trimerous perianth lobes, the other two being represented by the palea keels.

Palea

The palea is a membranous leafy organ situated opposite the lemma, showing a distichous arrangement. The vascular traces of both lemma and palea arise from the axial strands at about the same level, indicating a possible whorled arrangement (Figs. 43, 45). The palea and the lemma are arranged in such a way that the caryopsis and the remaining floral parts are completely enclosed. The bikeeled palea has two conspicuous vascular bundles. The anatomical details of palea of wild oats are similar to those described for cultivated oats (Bonnett 1961). The palea in wild oats, however, is interpreted as a compound structure made up of two lobes which can be recognized during their ontogeny. In later stages of development, the two lobes become laterally fused to form a single structure. Therefore, each keel of the palea can be considered as an independent palea lobe.

In wild oats, the palea is interpreted as a compound appendage whose two lobes share together with the large lemma to organize the perianth whorl of the floret. Because of the presence of a single whorl of perianth the floret can be regarded as monochlamydeous.

Lodicules

Considerable controversy revolves mostly around the lodicules in any discussion of grass floret morphology (Arber 1934; Bonnett 1961; Clifford 1961; Guédès and Dupuy 1976; Kam 1974; Maze et al. 1971; Mehlenbacher 1970; Pizzolato 1983). Many interpretations have been advanced about the morphology of the lodicules, but the most commonly mentioned view (although not one accepted by all), is that they represent the two perianth lobes, the posterior one being absent. Based on their ontogeny, Mehlenbacher (1970) regards the lodicules as intermediate between foliar organs and stamens.

The floret of many grasses, including wild oats, contains two lodicules placed in the antero-lateral part of the floret on

either side of the anterior stamen. The posterior lodicule is absent in the florets. It is not uncommon to find many stamens arranged in whorls in the florets of bamboos (Arber 1934). In *Oryzopsis* the posterior lodicule appears shortly after the formation of palea and is placed presumably inner to the palea (Maze et al. 1971). If such a posterior lodicule were to appear in wild oats, it must then occur inner to the palea, between the keels of palea. The two anterior lodicules in wild oats are placed on either side of the anterior stamen and, together with the third (posterior) lodicule, which perhaps has evolutionarily been suppressed here, would form a trimerous whorl of lodicules. Such lodicules would then alternate with the outer trimerous whorl of perianth made up of two postero-lateral keels of palea and the anterior lemma.

Each lodicule receives a single vascular trace which branches to form many bundles. Such vascular bundles are not well differentiated within the lodicules, which are transitory structures in wild oats. The lodicules seem to serve the function of anthesis when the lemma of the floret is stretched out by the radial enlargement of lodicules caused by water uptake (Raju et al. 1984). Often, the enlarged lodicules burst, and persist as rudimentary membranous structures during post-fertilization stages of florets. The occurrence of well-differentiated vasculature, including tracheary elements, is known to occur in lodicules of some grasses (Arber 1934; Pizzolato 1980a, 1983; Zuderell 1909); stomates are also developed in the lodicules (Pizzolato 1980b).

The topography or position of lodicules in the floret, the entrance of a single vascular trace into the lodicule, and occasional development of stomates in them suggest that the lodicules may be regarded as a modified outer whorl of stamens and that they are specialized for anthesis in some grasses, including wild oats. The stamens in wild oats, as in the lodicules, contain poorly developed vasculature in their filaments and stomates (presumably nonfunctional) in the connectives of anthers (Fig. 80).

Stamens

Three stamens showing a trimerous whorl are situated around the pistil in a wild oat floret (Figs. 65–71, 77). The anterior stamen is situated between the anterior lodicules. The other postero-lateral stamens are placed inside and opposite the keels of palea, which are the perianth lobes. The presence of such antitepalous stamens in a whorl indicates obdiplostemony, which is a characteristic stamen arrangement in flowers of some families of dicots (Lawrence 1951; Puri 1951; Raju 1953). Thus, the floret of the wild oat can be interpreted as having two whorls of stamens. The outer whorl of stamens is modified into lodicules, the posterior lodicule being absent, and they alternate with the outer perianth lobes (lemma and two keels of palea). The inner whorl of three functional stamens, which are situated opposite the perianth lobes, alternates with the lodicules. Each functional stamen has a short filament and a distal elongated quadrisporangiate anther. The connective of the anther is well-differentiated; often, many stomata develop on its adaxial side. At, or immediately after, anthesis, the anthers dehisce laterally, releasing pollen. Simultaneously, the filaments stretch into fine strings with the empty anthers still attached. Spikelets are usually pendant at this time.

Pistil

The morphology of the pistil of grasses has received the attention of morphologists and taxonomists for a number of years, but they have focussed particularly on two problems. The first is the number of carpels associated with the pistil, one or many (two, three, or four). The second problem concerns the position of the single ovule. Is the ovule terminal (stachysporous) or lateral (phyllosporous) in position? These problems have been succinctly analyzed and discussed (Kam 1974; Maze et al. 1971; Philipson 1985).

The spikelet of wild oats is a determinate inflorescence. The floret, therefore, is a terminal organ and the apical meristem of the floral axis is completely used up. My study provides further evidence to support the view that the unilocular pistil of wild oats is pseudomonomerous, derived developmentally from a tricarpellary condition. The single

ovule associated with the pistil is appendicular (phyllosporous). Although there is considerable criticism concerning the use of data from floral anatomy in solving morphological problems (Carlquist 1969), it is still possible that evidences based on shrewd observation and judgement help in presenting reasonable morphological interpretations.

In the florets of wild oats, after the stamen traces have diverged from the axial stele (strands), the remaining axial strands of the stele of the pedicel (of the pistil) extend distally and produce carpellary traces which eventually become the carpellary bundles (Figs. 56–62, 65–72). Unfortunately, it is difficult to find well-differentiated vascular strands, especially in the young pistils, until after double fertilization in the embryo sac has taken place. In a few cases at the pre-fertilization stages, it is possible to find cells vaguely resembling the provascular strands. I have based my interpretations on such instances, and my interpretations have been confirmed by observations made on sections of florets in different post-fertilization stages.

The pistil of wild oats has an ascidiate morphology like other grass-related forms (Philipson 1985). At about the stage when the ovule is already initiated, the provascular strands are not visible (Figs. 58–60). The carpels are free in the more distal region on the adaxial side of the pistil (Figs. 61–63). In pistils of this type, the stylar parts are obvious (Figs. 61–64). The provascular strands are differentiated better at about the stage when the ovule contains a mature embryo sac or post-fertilization stages (Figs. 102, 103). The lateral carpellary traces (C_1 and C_3 in Figs. 67–71) may remain connected to the axial strands to form a large commissural bundle, the outer (with reference to ovular strand) continues distally as the axial strand(s), and the inner as ovular strand supplying the ovule (Figs. 69, 70). The outer axial strand continues to extend distally for some distance and gradually fades out (Figs. 73–76). The ovular strand supplies the ovule and also remains associated with the axial strand. The carpellary axial part, with the axial strand along with the associated ovular strand, elongates considerably; both types of strands thus remain more intimately associated and cause the ovule or the developing

seed to change from a young orthotropous ovule to a mature hemi-anatropous condition. In later stages of seed development, the vasculature (xylem and phloem) in the axial and ovular strands becomes distinct. The ovule appears to be pendant, attached proximally to the modified region of the ovary wall or the placenta organized by the lateral ends or margins of the carpels C_1 and C_3 on the adaxial side (Fig. 76). The ovule, or the seed, is supplied by the ovular strand and the point of attachment of the ovule shifts from the more proximal region of the carpels, C_1 and C_3, to the more distal end of the carpels. The ovule, therefore, is interpreted as lateral in position to the carpellary margins or the axial strand (Figs. 66–71, 76).

Based on a comparative morphology of the pistil of grasses and other closely related taxa, Philipson (1985) concludes that the former has a tricarpellary ancestry and, therefore, the carpel associated with the grass pistil is pseudomonomerous (Eames 1961). In wild oats the single carpel associated with the pistil contains three traces or bundles, each representing a carpel. In most carpels the occurrence of three bundles per carpel is the norm, and the grass pistil contains only one carpel with three bundles in it (Kam 1974; Klaus 1966; Maze et al. 1971). There are also instances in some angiosperms where highly reduced carpels with fewer ovules can have one bundle instead of three (Puri 1951). In studies of organogeny in maize one can find the pistil arising from a single crescentic structure (Cheng et al. 1983). The rim of this structure does show an uneven surface with three possible ridges, which may represent three independent carpels involved in the pistil; therefore, the crescentic structure must be a compound structure. In the wild oat a young pistil in cross section shows a plicate morphology (Figs. 59–61, 77) suggesting that it is made up of three carpels. In a separate organ, such as the palea, two independent primordia arise which later undergo lateral fusion during development resulting in a two-keeled mature organ; each keel contains a single vascular bundle. Thus, the organogenic pattern may change or become modified during development of the organ to maturity. Furthermore, C_1 and C_3, the two lateral traces in the pistil, contribute to the two

styles. There is no style differentiated as such on the abaxial side of the pistil, and the C_2 trace, which normally supplies the anterior (abaxial) style if there were an abaxial style, fades out within the carpellary wall before reaching the distal part of the pistil (Figs. 61–64, 71–76). These facts support the view that the grass pistil, at least in wild oats, is tricarpellary and unilocular, conforming to the pseudomonomerous type (Eames 1961).

As regards its position, the ovule of wild oats arises in the placenta on the ventral side of the pistil. It appears in the region of the fused margins of the lateral carpels, C_1 and C_3. In a cross section of the pistil, the bundles C_1, C_2, and C_3 represent the bundles of three carpels, and the fourth bundle in the adaxial position is the adaxial or posterior commissural bundle made up of the outer axial strand and the inner ovular trace (Figs. 56, 61, 65–71, 76). The axial strand continues distally and the inner ovular trace supplies the ovule. Because of the longitudinal growth in the pericarp, the ovular strand remains conjoint with the axial strand for some distance, and then moves inwardly into the ovule (Figs. 76, 99, 101). As it is supplied by a separate ovular strand and placed inside (toward the carpel), the ovule can be interpreted as a lateral and not a terminal organ. Therefore, the ovule in the pistil of wild oats, and possibly in other grasses, is phyllosporous. My interpretation contrasts with the view of others (Bonnett 1961; Kam 1974; Maze et al. 1971; Mehlenbacher 1970), who consider it as stachysporous.

The floret of wild oats (*Avena fatua*) is a monochlamydous structure consisting of trimerous floral parts. The outermost whorl, the perianth, is made up of a large anterior lemma and two postero-lateral lobes or keels which have conjointly fused to form a compound organ, the palea. Alternating with the perianth lobes are the lodicules, which number two in wild oats. They are situated in the anterolateral position, still vascularly recognizable as alternating with the lemma and palea lobes (keels). The posterior lodicule, which might be expected to be present between the two keels of the palea, is absent in wild oats. The three functional stamens form the next inner whorl, and are situated opposite the perianth

lobes (two palea lobes and one lemma), and remain alternate with the lodicules. The last internal whorl is made up of three carpels which together organize an unilocular compound pistil with two stylar branches, each terminating in plumose stigmatic branches (Bonnett 1961; Raju et al. 1985). My interpretation is that the anterior or abaxial carpel with its single vascular bundle aborts in wild oats.

The initiation organ whorls in a floret follows the sequence — *lemma* + *palea* → *lodicules* → *stamens* → *carpels* (pistil). This sequence is based on the level at which the vasculature diverged from the axial strands toward the respective whorls of organs of a floret.

In the early stages of floret development, the occurrence of recognizable provascular tissue leading into the organs from floral axis is usually obvious. The differentiation of xylem and phloem in the provascular tissue is considerably delayed. During differentiation, the phloem tissue appears much earlier than the xylem. The xylem strands show considerable discontinuity, indicating their irregular differentiation, and this is further compounded by the irregular elongation of cells in the provascular tissue. However, in later stages of development, well-developed vascular elements appear, establishing xylem continuity. The extent of vascular elements, especially the xylem, is somewhat limited.

FLORET AND EMBRYOLOGY

Stamen and anther

In a wild oat floret there are three functional stamens, each with a short filament terminating in two long bilocular sporangia which are separated by a thick connective with a wider adaxial and a narrower abaxial parts; the former often contains stomata (Fig. 80). The anthers are greenish in the early stages of stamen development, and finally become yellowish because mature microspores are yellow. At the time of anthesis, the mature anther dehisces on its lateral sides releasing the yellow microspores. The filament of the stamen, although short in the beginning, becomes considerably elongated and protrudes from the floret. The organogeny and development of stamens are similar to those of cultivated oats (Bonnett 1961).

Microsporogenesis and male gametophyte

A transverse section of a young anther primordium shows a 4–lobed structure surrounded by a common epidermis (Figs. 77, 79, 88, 89). In each of the four lobes or sporangia, the subepidermal archesporial cell is differentiated (Fig. 88). The archesporial cell divides periclinally (tangentially) to form an outer primary parietal cell and an inner primary sporogenous cell (Figs. 78, 88). The primary parietal cell divides anticlinally and periclinally, resulting in three layers of cells of which the innermost becomes the tapetum, and the remaining two form the middle or wall layers (Figs. 79, 89–92). The primary sporogenous cell divides again in different planes, producing more sporogenous cells which subsequently differentiate into microspore mother cells (Figs. 93, 94). Thus, in each locule of a developing anther appears a group of primary sporogenous cells immediately surrounded by the nutritive layer or tapetum, whose cells may be uninucleate or binucleate. The tapetum, consisting of dense cytoplasmic cells, eventually becomes the main source of nutrition for the developing microspore mother cells and

microspores, and finally it becomes obliterated. During development of the anther, the inner of the two middle layers in each anther lobe is crushed, and the outer persists, differentiating into a specialized layer, the endothecium (Figs. 82, 94–97). The cells of the endothecium develop characteristic fibrous thickenings, and eventually become hygroscopic. The endothecium is known to aid in the dehiscence of anthers. The mature anther wall, at about the stage when microspores are formed, consists of an epidermis and a subepidermal endothecium (Figs. 82, 83, 96, 97) enclosing mature microspores. Along the lateral sides of the anther, the wall differentiates into the line of dehiscence or stomium through which, after dehiscence, the microspores are released.

The microspore mother cells mature and undergo meiosis to form microspores. Meiosis in these cells includes two successive divisions or cytokinesis producing microspore tetrads of the isobilateral type. The mature microspores at the time of anthesis or shedding are three-celled; each microspore is monoporate and contains a tube nucleus and two male cells (Figs. 86, 87, 96, 97). Different ultrastructural and histochemical changes during the development of microspores in angiosperms, including the Gramineae, have been reviewed extensively (Bhandari 1984; Knox 1984).

Pistil and ovule

The superior pistil (ovary) of wild oats is tricarpellary and unilocular, enclosing a single laterally placed ovule. The style is short, bifurcating distally to form two plumose stigmatic branches. The stigma is made up of a large number of multicellular papillae through which the pollen tube gains entrance.

The ovule is a remarkable organ in wild oats and in other grasses in that it is intimately associated with the ovary at various stages of development. Both these structures organize, after fertilization, a highly specialized type of fruit, the caryopsis. The ovule in grasses has been variously described as orthotropous, anatropous, hemianatropous, etc. (Davis 1966; Maze and Bohm 1977; de Triquell 1986). The angiosperm ovule structure, development and morphology

have recently been reviewed from a historical and general perspective (Bouman 1984). In a more recent review, de Triquell (1986) considers the mature ovule as morphologically uniform in the entire Gramineae, and that the morphological variations observed in grass ovules are due mainly to observations made at different stages of ovular development. In a schematic presentation of ovule development in grasses, de Triquell (1986) states that the change in the ovular axis is known to play an important role in determining the nature and morphology of the ovule.

In wild oats, the ovule arises as a nucellar primordium in the placenta, organized by the fusion of carpellary margins within the ovary locule (Figs. 59, 60, 70, 98). At about the stage of the archesporial differentiation, the initials of the inner and outer integuments are recognizable, and in their further development they partly envelope the nucellar primordium (Figs. 98, 99). In a mature ovule, the inner integument organizes the micropyle at the distal end of the nucellar primordium (Figs. 101, 102). The inner and outer integuments are mostly two-layered, except at the distal extremities, where they are three to four cells thick (Figs. 84, 85, 167, 168).

There is some difference of opinion whether the grass ovule is crassinucellate or tenuinucellate (de Triquell 1986). Both Maheshwari (1950) and Eames (1961) have distinguished the two types on the basis of the presence, or absence, of parietal tissue. The crassinucellate type is reported to contain many parietal cells, and the tenuinucellate type contains a few or none. Maheshwari and Eames also caution that the difference between the two types is not always sharp. The mature ovule in wild oats, at the time of anthesis, contains abundant nucellus and some parietal cells and, therefore, it is considered crassinucellate.

Basing his conclusions on some histological changes in the ovular axis, de Triquell (1986) suggests that the different types of ovule morphology can be traced back to some fundamental types of ovule proposed by Bocquet and Bersier (in de Triquell 1986). In the Gramineae, the ovular primordium with its short pedicel, which is very intimately associated with the ovary wall and placenta, becomes

significantly curved, showing an oblique axis (de Triquell 1986). On the other hand, Maze and Bohm (1977) consider that the ovule develops from the floral apex, indicating the cauline nature of the ovule. The initial change in the orientation of the ovule is due to growth in the region of the gynoecium below the level of the ovule attachment. As a result, the ovule is placed perpendicular to the longitudinal axis of the gynoecium. Subsequently, the ovule grows more on its upper side, near its basal end, resulting in a change from the early orthotropous condition to a hemianatropous morphology (Maze and Bohm 1977). Maze and Bohm (1977) have used the angle created by the two axes, one from micropyle to antipodal and the other from micropyle to the basal end of the extended embryo sac, to separate some grass taxa. Similarly, the position of antipodals in the embryo sac has been used to distinguish the Pooid grasses from the Panicoid grasses (Chandra 1963a). Unfortunately, both these methods appear to be erroneous as they require the right plane of the section for appropriate interpretation. The extent of antipodal tissue differentiation in the chalazal region is variable, and obtaining accurate measurements is difficult. It is surprising to learn that the antipodals could lie in the non-chalazal region of the panicoid ovules (Chandra 1963a, b)!

In a young ovary, the ovular primordium becomes situated perpendicular to the longitudinal axis of the gynoecium when the chalazal and micropylar ends of the ovule remain obvious (Figs. 98, 99). The provascular strand extending into the short pedicel of the gynoecium can be recognized at the chalazal end (Fig. 101). The chalazal end can be considered as the region of ovular attachment to the placenta (ovary wall). The funiculus, which is ordinarily seen in angiosperm ovules, is very short in wild oats (probably also in other grasses) and fused with the adaxial ovary wall.

During the transformation of a young ovular initial of the orthotropous type to the anatropous morphology, growth occurs both in the ovule and in the adaxial part of the ovary wall below the region of ovular attachment. The growth in both sites is brought about by cell division and elongation. Growth by cell division is more in the ovule than in the ovary

wall; cell elongation in the ovary wall is more prevalent. As a result of growth in the adaxial part of the ovary wall, the site of ovular attachment (chalazal end of ovule) is lifted up toward the distal end of the ovary (Figs. 101–103). Considerable cell division and elongation also occur in the provascular strand making it more robust (Figs. 102, 103). Surprisingly, even at a stage when the mature embryo sac is seen in the nucellus of the ovule, no extensive differentiation of xylem and phloem is observed in the massive provascular strand. This is deferred until after anthesis of the floret (Figs. 99, 102). If there is any vasculature present prior to anthesis, it is usually minimal and discontinuous. However, in later stages of seed development continuous or uninterrupted strands of vasculature are differentiated (Figs. 69–71, 76, 103). These vascular strands, especially at the base of the ovule, are the commissural strands, which include both the ovular strand and the remains of the axial vascular strand.

While the ovule is changing to the anatropous condition, both cell divisions and cell elongation occur in the nucellus and integuments. The nucellar tissue is substantially increased, and the integuments also grow to keep pace with the enlarging nucellar tissue. During the longitudinal extension of the adaxial part of the ovary, the growth of the integuments on the adaxial side is physically restricted; this part of the integuments in contact with the ovary wall becomes obliterated (Figs. 102, 103). On the other hand, the integuments, that are not in contact with the adaxial side of the ovary wall, grow normally, and they may show overgrowth, shifting the micropyle to an oblique position. Thus, in a sagittal section the ovule may appear anatropous, campylotropous, hemianatropous, etc. Despite these changes in the ovary wall and the ovule, the positions of the chalaza and the micropyle in the ovules remain the same, i.e., opposite to each other, at least until the time of double fertilization in the embryo sac. The mature crassinucellate ovule in wild oats is basically anatropous and its micropyle is organized only by the inner integument (Fig. 102). The ovule within the locule of the ovary appears pendant as the chalazal part of the ovule is shifted to a more distal region

from the earlier proximal position in the ovary (Figs. 102, 103). The ovule fills the entire ovary locule.

The developmental changes in the female gametophyte do not seem to have any significant and direct effect on the change in morphology from young orthotropous to mature anatropous condition, nor on the shifting of the ovule from the proximal to the more distal region. Post-anthesis stages in the embryo sac, including double fertilization, can influence the shape and size of the ovule and seed (fruit), however.

Megasporogenesis and female gametophyte

A considerable amount of information is available about the embryology of grasses (see Davis 1966; de Triquell 1986; Johri 1984; Willemse and van Went 1984). However, no major papers on the embryology and morphology of wild oats have been published since Cannon's first work (1900).

One of the subepidermal cells in the distal part of the nucellar primordium differentiates into an archesporial cell (Fig. 104). In most instances, the archesporial cell functions directly as the megaspore mother cell (Fig. 77). In a few cases, the archesporial cell may divide periclinally to produce an outer parietal cell and inner primary sporogenous cell (Fig. 105). The primary parietal cell may divide periclinally and anticlinally to form a few cells of the parietal tissue, which eventually become crushed by the enlarging embryo sac. These crushed cells may persist in the region distal to the primary sporogenous cell as darkly stained bodies (Figs. 105, 107, 108). The primary sporogenous cell becomes the megaspore mother cell (Fig. 108), and undergoes reduction division to form a linear or a T-shaped tetrad (Fig. 107) of megaspores of which the most proximal or chalazal megaspore develops into an embryo sac (Fig. 109). Occasionally two linear tetrads, possibly derived from two megaspore mother cells, may develop (Fig. 110). In all cases, the chalazal or the lowermost megaspore becomes functional, and undergoes three mitotic divisions to produce the eight nuclei of the embryo sac (Figs. 85, 86, 109–144). As in many other grasses, the pattern of embryo sac development in wild oats conforms to the Normal or Polygonum type (Maheshwari

1950). The eight nuclei arrange themselves, dictated by polarity, to organize a micropylar egg apparatus and chalazal antipodal cells (Figs. 86, 113, 114). The egg apparatus in the mature embryo sac is composed of two synergid cells and an egg cell. At the chalazal end, the antipodal cells divide repeatedly to form many cells (maximum counted in my study was 14) some of which may penetrate into the chalazal tissue and behave as haustoria (Fig. 87, 116). Some antipodal nuclei become highly hypertrophied with many nucleoli and with dense cytoplasm, especially before fertilization, suggesting probable high metabolic activity (Figs. 86, 87, 116). The antipodal cells may also divide to form a compact tissue in the chalazal region of the embryo sac (Fig. 113). The function of such a tissue is not known currently. The large central cell of the embryo sac contains two polar nuclei which remain separate until about the time of triple fusion, when the two polars, chalazal and micropylar, fuse to form the secondary nucleus, which is immediately fused by the male cell. This results in the primary endosperm nucleus (Figs. 114, 115).

Pollination

Autogamous pollination is known to occur in many grass taxa, including wild oats (Connor 1986; Harlan 1945; Raju et al. 1985; Smith 1944; Stebbins 1974). In wild oats, the occurrence of pollination is signified by anthesis or opening of the florets. This opening of florets, including the divergence of the lemma away from the palea, is brought about by the radial enlargement of lodicules in the florets.

The florets of wild oats always open in the afternoon, whether in the field or in the environment-controlled growth cabinets (Raju et al. 1985). It is not clear now if there is a circadian rhythm in this process, or whether a certain number of hours of light are needed for the florets within the spikelets to open. Nevertheless, the opening-closing is a one-time performance; when once the florets have opened and closed, they cannot repeat the process. The lodicules, after maximum swelling, help in anthesis, and rupture themselves, resulting in the closure of the floret. The lodicules become damaged and do not swell again.

Just before anthesis, when the floret is still closed, a considerable amount of humidity is built up within the floret. When anthesis occurs, the mature anthers are suddenly exposed to low humidity in the environment. This change in humidity can cause dehiscence in anthers, especially in the region of stomium, and clouds of microspores are released. This humidity change can also make the feathery stigmas of the pistil flare out, thus capturing the pollen dust. The filaments of stamens also stretch, pushing the anthers out of the floret at the same time. If the divaricate florets (spikelets) in the panicle are downwardly directed, a feature which is normal to them, the anthers drop down, still attached to the filaments. Gravity may make the filaments stretch further, and the anthers remain dangling in air even after the florets have closed.

The pollen come in contact with the stigmatic papillae, effecting pollination in florets. The pollen can germinate on the stigmatic papillae only after the process of anthesis has been completed. Pollination in wild oats is essentially autogamous, but allogamy is not completely eliminated. The occurrence of both geitonogamy and xenogamy are not impossible in florets under certain circumstances. Although the florets of wild oats are predominantly chasmogamous, results of some experimental study show that they are not obligately chasmogamous (Raju et al. 1985).

Each spikelet contains two to three florets; the proximal two are generally functional and produce viable seeds. The time of anthesis in them is not the same. The primary floret, which is initiated the earliest, opens first, and this is followed by the second, and possibly by the third. Similarly, many developmental changes, that are common to all, are somewhat staggered in time. The changes occur first in the primary floret, and then in a sequence in others, with a time difference of about one day. For example, the process of double fertilization observed in the primary floret, may be seen after a day or two in the second floret. It is not impossible, however, to find these processes occurring concurrently in the primary and secondary florets. Such exceptions are seen between primary and secondary florets, but not in any other sequence with the third floret. Based on

these observations and others, I assume that the primary floret of wild oats can develop and mature better than the others.

Double fertilization

The process of double fertilization, which includes syngamy and triple fusion, is similar in wild oats (Fig. 115) to the one described for cultivated oats (Bonnett 1961). Ultrastructural and biochemical changes during germination of pollen tube into the stigma in angiosperms have been described in detail by Knox (1984) and by van Went and Willemse (1984). The mature microspores of wild oats, released during anthesis, come in contact with the stigmatic papillae. These three-celled monoporate spores germinate and the pollen tube penetrates the stigmatic papillae, carrying into it the two male cells and a tube nucleus. The pollen tube in wild oats migrates intercellularly into the stigmatic branches and then into the transmitting tissue of the style. Finally, the pollen tube carrying the degenerated tube nucleus and the two functional male cells, enters the ovular micropyle, and penetrates the mature embryo sac. During its entry one of the synergids in the embryo sac seems to be destroyed and the other persists for about 18 to 28 hours after anthesis. Meanwhile, one of the male cells (nuclei) will have fused with the egg cell (nucleus) bringing about syngamy. The second male cell (nucleus) comes in contact with one of the polar nuclei in the central cell of the embryo sac. The two polar nuclei remain free until the contact is made by the male nucleus when a simultaneous triple fusion is effected (Fig. 115). Thus, in the embryo sac the zygote is formed as a result of syngamy, and a primary endosperm nucleus is produced by triple fusion of two polar nuclei and one male nucleus (Fig. 115). At this stage of double fertilization, the antipodals seem to show maximum activity and enlargement of nuclei and cells; the stainability of cells also increases considerably (Figs. 86, 87, 113–116). They are also known to be matabolically active at some stages of embryo sac development, especially at the mature embryo sac stage and immediately after fertilization. The antipodal cells may behave as absorbing or haustorial cells

(D'Amato 1984; Johri and Ambegaokar 1984; Willemse and van Went 1984). The structure and function of the antipodal cells have been investigated extensively in dicots. However, no such studies are conducted on antipodals in grasses despite the fact that the cells become large, multiply to produce many cells, the nuclei are highly polyploid, and their chromosomes become polytenic (D'Amato 1984). In wild oats, the antipodal cells are situated close to the chalazal nucellar tissue (often called "hypostase") where the ovular vascular strand usually terminates in the ovule. It is possible to envisage some kind of absorbing function for the antipodal cells. In wild oats, the antipodal cells in some instances penetrate deeper into the subjacent nucellar tissue and, therefore, an absorbing or a haustorial function can be ascribed for these cells.

Double fertilization in the embryo sac brings about many changes in the embryo sac and the tissues around it in the ovule and the ovary. Four major changes can be identified: (1) the zygote develops into an embryo which is, of course, a normal process of development; (2) the primary endosperm nucleus eventually produces a massive endosperm tissue; (3) the embryo sac enlarges along with the endosperm to such an extent that the outer tissues, both of ovule and of ovary, become highly compressed, modified or obliterated; (4) the final change is the gradual degeneration and final obliteration of antipodal cells within a few days after double fertilization. These broadly circumscribed changes result in the development of a specialized structure, the seed, or more appropriately in grasses, including wild oats, the caryopsis. These changes occur very rapidly. For example, anthesis normally results in pollination, and within 12–18 hours after anthesis double fertilization is achieved. In about 24 hours after anthesis the primary endosperm nucleus will have produced several endosperm nuclei.

EMBRYO DEVELOPMENT

From a historical and evolutionary perspective, the structure and development of monocot embryos, including grass embryos, have been interesting and controversial. In an excellent recent review some important problems relating to embryos, both monocots and dicots, have been selected and discussed (Natesh and Rau 1984). Although investigators in the past emphasized the differences between monocot and dicot embryos, it is now clear from the extensive publications of Souèges (in Davis 1966) that, despite the occurrence of differences in mature embryos, the early stages of development and the sequence of segmentation patterns in the embryos of both monocots and dicots are very similar. In more mature embryos, however, the associated organs are so disposed that it is possible to find important differences. Monocots, as the name suggests, contain a single terminal cotyledon in the embryo, whereas the embryo in dicots has two laterally placed cotyledons, one on either side of the epicotyl. In embryology, the various histogenic patterns of embryos established by Souèges (see Davis 1966; Johansen 1950; Natesh and Rau 1984) have been applied to trace cell lineages and destinations of some parts of the embryo. Although some investigators (Swamy and Padmanabhan 1962; Wardlaw 1955, 1963) are critical of such histogenic studies based on embryonic laws (Johansen 1950; Natesh and Rau 1984), these studies remain useful in providing information about common morphological features among the major taxa of vascular plants. Studies of this kind may also aid in advancing broad generalizations and interpretations with respect to the inter-relationships and evolution of plant groups. Burger's research on the comparative morphology of embryos of different vascular plant groups (Burger 1977, 1981) has provided evidences to advance the view that monocots are indeed primitive; the

similarities, morphological or otherwise, between monocots and non-angiospermous vascular plants are much greater than between dicots and non-angiospermous vascular taxa. In the angiosperm group itself, more evidence is being put forward to question the concept that the monocot and dicot embryos differ significantly in the number and position of the cotyledons in the embryo (Haccius 1952; Lakshmanan 1972; see Natesh and Rau 1984; Swamy and Lakshmanan 1962; Swamy and Parameswaran 1962). One of the controversial monocot groups often considered in such phylogenetic discussion has been the Gramineae (Clifford 1970).

The zygote (Fig. 117a) divides transversely to form an apical cell, *ca*, and a basal cell, *cb*, about one day after fertilization (Figs. 117a, b). The basal cell divides again transversely resulting in two tiers of cells, *m* and *ci* (Figs. 117c, d). The cell, *ca*, undergoes two longitudinal divisions, one at right angles to the other, to produce four cells or quadrant, *q* (Figs. 117c–e). A transverse division in the quadrant results in an octant (Fig. 117f). The tiers, *q*, *m*, *and ci*, can divide many times to form a massive proembryo (Figs. 117g–k). The divisions are often nonsynchronous and, consequently, it is rather difficult to follow cell lineages and destinations. About 5 days after anthesis, a massive multicellular embryo is developed in which it is possible to recognize three regions, the distal, the middle, and the proximal, and these can easily be traced back histogenically to *q*, *m*, and *ci* seen in a young proembryo (Figs. 117j–m). Such histogenic demarkation, recognizable in a massive embryo, may not represent functional or organ specificity. There is always overlapping of cells or regions, and so too with the functions. Histogenic studies, nevertheless, are useful in establishing structural patterns in any comparative study of a large number of taxa. Identification of similar patterns in embryo development has enabled Souèges (see Crété 1963; Natesh and Rau 1984; Rau 1954) to formulate important megarchetypes. Similarly, by following the developmental patterns of embryos, Johansen (1950) has recognized and and provided simpler classifications for a few types. The development of the wild oat embryo, with some

modification, follows the Asterad type-Poa variation (Johansen 1950).

Of the three tiers (or zones) in a 5-day-old proembryo (Figs. 117l, m) the *q* produces most of the cotyledon (scutellum). The tier *m* is significant as it is responsible for the formation of important parts of the embryo, such as a part of scutellum, stem tip, first leaf, root-tip and root-cap. The most proximal tier *ci* (Figs. 117l, m) can divide and produce more tiers (Figs. 117l-q). Nevertheless, this tier produces the coleorhiza, suspensor and epiblast. The parts of a normal embryo, such as scutellum, shoot apex, coleoptile initials, etc., become recognizable in the embryos about 8–9 days after anthesis. Concurrent fast developmental changes also occur in the endosperm associated with the embryo.

In a 5-day-old proembryo, the simultaneous initiation of shoot and root apical meristems becomes obvious in tier or region *m* and establishes polarity, the shoot apical meristem placed distal to *m* and the root apical meristem proximal to it (Figs. 117m–o). The tier *q* distal to *m* contributes partly to the massive scutellum and to the upper part of the coleoptile (Figs. 117k–o). The lower part of *q* on the abaxial side of the proembryo is continuous with the tier *m* on the same side (Figs. 117l, m, o, 121, 122). Therefore, the scutellum may be interpreted as being derived from *q* and also *m*, and situated lateral to shoot apical meristem. On the adaxial side of the embryo arises the lower part of the coleoptile. The first leaf takes its origin in the proembryonic tissue in the *m* tier (Figs. 117o–q). The first leaf is placed opposite the scutellum and is well recognizable in later stages of embryo development (Figs. 117o–q).

The root apical meristem (*Rm* or *Ra*—equivalent to *tec*) is initiated in the proximal part of *m*, and is placed opposite the distal shoot apical meristem (Figs. 117m, o). Eventually, it produces the primary root and root-cap (Figs. 117p–t). Subjacent (proximal) to the root meristem, *tec* (Souèges 1924), is the *ci* tier of the proembryonic tissue, suggesting that the primary root has an endogenous origin (Figs. 117m–t). The tier or region *ci* totally produces the coleorhiza, whose distal (basal) part is the suspensor. The epiblast, a membranous flap developed on the adaxial side of the

embryo, is an extension of the tier *ct* (coleorhiza) on its adaxial side; it is placed opposite to the scutellum in an older embryo (Figs. 117q–t, 118). In 8–9 days after anthesis the embryo contains all the different parts (although not fully developed) (Figs. 123, 124), that are normally seen in a mature embryo (Figs. 118–121, 125, 126).

The histogenic description of early stages of wild oat embryos corresponds to that described for *Poa annua* by Souèges (1924), although some differences exist, both in structure of the embryo and interpretation between the two taxa exist. The histogenic descriptions for the two taxa may be summarized in the following manner:

Poa annua (Souèges 1924)—

Zygote *ca* *q*: cotyledon (scutellum) + coleoptile (part).
(*pco*) (*cl'*)

cb *m*: stem tip (apical meristem) and first leaf
(*py*)
+ hypocotyl + root tip (apical meristem)
(*phy*) (*iec*)
+ coleoptile (part)
(*cl'*)

ct: coleorhiza + suspensor+root cap + epiblast
(*cr*) (*s*) (*co*) (*e*)

Avena fatua (present study)—

Zygote *ca* *q*: cotyledon (scutellum) (part)+ coleoptile (part)
(*Sc*) (*Cl'*)

cb *m*: cotyledon (scutellum) (part)+ coleoptile (part)
(Sc) (*Cl'*)
+ stem tip (apical meristem) + hypocotyl
(*Sa*) (*Hy*)
+ root tip (apical meristem) + first leaf
(*Rm* or *Ra*) (L_1)

ct: coleorhiza + suspensor + epiblast + root cap
(*Cr*) (*Su*) (*Ep*) (*Co*)

The early histogenic sequence of embryo development in *Avena fatua* does show a pattern that is comparable to the patterns reported for other grass taxa (Narayanaswami 1955, 1956; Souèges 1924). While investigating the rice embryogenesis in culture, Jones and Rost (1989) reported

that the early cell division stages in the proembryo do not follow any definite pattern. This conclusion is not surprising, as the ambient environment found in the embryo sac is conspicuously lacking under cultural conditions. In the wild oat, by contrast, the pattern of early embryo development was consistent in many different ovules.

The embryonomic formula presented for wild oats differs from that of *Poa annua* (Souèges 1924) in one fundamental way. Souèges (1924) considers the cotyledon (scutellum) as terminal to shoot apex and it is entirely derived from the quadrant *q*. In wild oats, on the other hand, the tier *q*, which is placed distally to shoot apical meristem, gives rise only to a part of the scutellum and the rest of it comes from the abaxial part of m. This suggests that the scutellum, in its entirety, is not a terminal organ, but it is situated laterally to the shoot apical meristem.

While she was studying the embryology of *Ottelia alismoides*, a monocot of the family Hydrocharitaceae, Haccius (1952) challenged the generally accepted view that the monocot embryos have a terminal single cotyledon. She suggested that the cotyledonary initial and shoot tip are differentiated side by side. Of late, more evidence has accumulated to show that the shoot tip in some monocots is, indeed, terminal (Lakshmanan 1972; Swamy and Lakshmanan 1962). My histogenic study of the embryo, although different from other investigated species of monocots (possibly other grass embryos), shows the presence of a terminal shoot apical meristem and a lateral cotyledon (scutellum).

The wild oat embryos show certain histogenic and morphological features, most of them common to other investigated grass embryos (Bennett 1944; Bonnett 1961; Chandra 1963a,b; La Rue and Avery 1938; Merry 1941; Narayanaswami 1956; Randolph 1936; Souèges 1924). Some differences of interpretation exist as to whether there are one or two cotyledons. The scutellum of a grass embryo is generally regarded as the only cotyledon, although its morphological interpretations are varied (Brown 1960, 1965; Dahlgren et al. 1985; Eames 1961; Natesh and Rau 1984). If the grass embryo is considered to have two cotyledons, there

is also the possibility of different views about the recognition of an organ homologous to the scutellum. For example, some researchers consider the epiblast or coleoptile as the second cotyledon (see Brown 1959, 1960, 1965). In the wild oat, the scutellum is, no doubt, equivalent to a cotyledon which has undergone both structural and functional specialization (Eames 1961; Negbi 1984; Negbi and Sargent 1986; Rao and Raju 1985). It is basically derived from the proembryonic tissue, and in its position the scutellum establishes the scutellar node on the embryo axis. The provascular tissue (vascular tissue) of the scutellum is proximally continuous with that of the hypocotyl. The first leaf primordium, placed opposite the scutellum in the embryo, is also derived from the proembryonic tissue. This later develops into the first leaf of limited growth (Figs. 117o–s). Furthermore, it is vascularly connected with the hypocotyl, and its vasculature proximally ends at the scutellar node, opposite to that of the scutellum. Therefore, the embryo of wild oats, which contains a laterally placed scutellum (first cotyledon) and the first leaf (second cotyledon), is morphologically not different from a dicot embryo.

The massive proembryonic tissue of wild oats and of other investigated grass taxa, in which different parts of the embryo are differentiated, resembles the proembryonic tissue of some gymnosperms (cycads, *Ginkgo*, and some conifers). The ontogeny and early development of proembryonic tissue in gymnosperms are fundamentally different from those of angiosperms in many respects. In gymnosperms, the proembryonic tissue has a free-nuclear origin in contrast to angiosperms where it is *ab initio* cellular. Nevertheless, the primary root of endogenous origin occurs in both, and the root is distally surrounded by the proembryonic tissue (coleorhiza in grasses) which fails to contribute to the embryo proper in either gymnosperms or grasses. At the proximal part of this tissue (away from the tissue in contact with the root tip) of this tissue is a small, few-celled suspensor, whose function is variable. This comparison of proembryonic tissue is made to indicate that grass embryos do carry some traits seen in primitive plants.

A comparative survey of dicot embryos indicates that there is a good correlation between extensive or specialized embryo suspensor development and a limited or poor development of endosperm or nutritive tissue in the developing seed. The suspensor in these cases behaves as a suctorial tissue, transporting nutrients to the embryo from other storage tissues (Johri and Ambegaokar 1984; Maheshwari 1950; Malik et al. 1980; Natesh and Rau 1984). On the other hand, in grasses, including wild oats, abundant endosperm is available at all stages of embryo development, and consequently the suspensor is developed as a few-celled, insignificant part of a massive proembryo (Figs. 117 p,q,s). The other function of a suspensor seems to be to push the embryo toward regions of stored nutrients. In fact, this is the situation in many pteridophytes, as claimed by Burger (1981). This is probably the only major function in these plants because the absorption or the haustorial function is performed by other regions (organs) of the embryo, such as the "foot" in the embryos of these plants. Therefore, it is no surprise to find the suspensor situated at an angle to the embryo axis (Gifford and Foster 1989). In angiosperms, especially sympetalous dicots, on the other hand, both suctorial and thrusting functions are performed by the suspensor (Davis 1966; Maheshwari 1951) and consequently the suspensor forms the proximal pole of the uniaxial embryos. In grass embryos, the suspensor appears to be a relic or rudimentary structure without any special functional significance. The scutellum of the embryo is specialized as a suctorial organ, and this organ occurs in all grass embryos.

The proembryonal tissue of grasses, situated between the primary root and the suspensor, is transformed into the coleorhiza in later stages of embryo development. It is a unique structure protecting the primary root, and it occurs in all grass taxa. The significance of its occurrence in grasses is not well understood. This tissue contains stored nutrients at all stages of development and, therefore, it may have a role in the regulation, physically and/or physiologically, of primary root growth during caryopsis germination. The presence of such a massive proembryonic tissue may have some evolutionary significance also. Probably the ancestors

of present-day monocots had large masses of proembryonic tissue. In grasses, this may represent a relic tissue, which later transforms into coleorhiza, protecting the primary root, as the embryo in a caryopsis is not buried in endosperm, neither is the seed coat well developed. It may also have a role in root emergence during caryopsis germination (Raju et al. 1988b).

I interpret the scutellum and the first leaf as homologues placed opposite to each other at the scutellar node. They are morphologically different and seem to be concomitant with their respective different physiological specializations. In wild oats and other grasses, the scutellum plays an important role in mobilizing nutrients from endosperm to embryo in the early stages of embryo maturation until the establishment of seedlings. Subsequently, the first leaf (second cotyledon) of the seedling begins to supply nutrients by photosynthesis. This mode of nutrient supply through the scutellum and the first leaf at different stages of embryo and seedling development is important in the success and survival of wild oats in the field. This mechanism applies to other grasses as well. In seeds germinating at greater depths, maximum exploitation of reserve food by their scutella is a necessity until seedlings emerge above ground (Negbi and Sargent 1986). After the seedling has emerged and its first leaf is above ground, photosynthesis in the leaf assumes the function of nutrient supply analogous to the mobilization of nutrients from the seed by the scutellum.

ENDOSPERM DEVELOPMENT

Anthesis in wild oat florets, as in other grasses, brings about pollination. Within about 24 hours after anthesis double fertilization occurs in the embryo sac. This process triggers tremendous changes within the embryo sac and outside in the ovule and the ovary. Syngamy and triple fusion, two important complemental processes, result in the development of the embryo and the endosperm, and culminate, with other associated changes, in the seed or caryopsis. The development of endosperm precedes that of the embryo so that the latter has an access to nourishment for its growth.

During double fertilization the second male nucleus fuses with the two polar nuclei to form a triploid primary endosperm nucleus. This soon divides repeatedly to form many nuclei (Figs. 127, 151, 152). Within a day after anthesis the embryo sac may contain about 8 free nuclei associated with the fertilized egg (Fig. 151). The antipodal cells, which were highly conspicuous in the mature embryo sac prior to anthesis, now begin gradual degeneration (Figs. 151–154). Many changes that occur within and outside the embryo sac can be observed easily in sagittal sections of florets.

Following double fertilization, the embryo sac elongates considerably, obliterating the nucellar tissue in the ovule. The position of the antipodals, i.e., close to chalaza, remains about the same. Divisions in the endosperm nuclei result in more nuclei. The ovule stretches longitudinally, and, at the same time, the adaxial part of the ovule associated with the pericarp (ovary wall) also stretches. Consequently, the antipodals get crushed, and their remains appear laterally in the embryo sac (Figs. 153, 154). The chalazal part of the nucellus, where the vasculature of the ovule terminates the nucellar cells, becomes thick-walled to organize the

"hypostase" (Maheshwari 1950). Because the ovary wall stretches on its adaxial side, the ovular strand associated with the ovary wall also stretches longitudinally. The entire ovule appears pendant and anatropous, and its adaxial part is firmly apposed with the carpellary wall (Figs. 153–154). The position of the antipodals may also shift more toward the distal end of the ovary (pericarp). The hypostase, which remains associated closely with the common vascular bundles of the ovule and floret axis (axial strand), becomes conspicuous and contributes to the formation of the "adaxial groove" (Figs. 103, 153, 154, 176). In addition to this stretched hypostase, the groove also contains obliterated nucellar and antipodal cells, and other cell degradative products which give the groove a dark-brown colour. This coloured groove, consisting of heterogenous tissues, may be compared to the often described "pigment strand" in some cereals (Zee and O'Brien 1970).

While tissue changes are going on in the ovule and the ovary following double fertilization, the embryo and endosperm develop within the embryo sac. A large number of endosperm nuclei are formed, and the divisions show no synchrony in endosperm in the embryo sac. These endosperm nuclei are scattered in different areas of the embryo sac, primarily because of the elongation and distention of the embryo sac, and its encroachment upon the surrounding nucellus. Nevertheless, the endosperm nuclei closely abut against the embryo sac membrane all around. In areas of antipodal and chalazal tissue cytoplasmic strands of nuclei, often from adaxial and abaxial sides of embryo sac, appear very closely placed (Figs. 139, 143, 153, 154). However, in the micropylar end of the embryo sac the free nuclei densely aggregate around the proembryo (Figs. 151–153). Three to four days after anthesis cell walls begin to appear between the endosperm nuclei, especially in the micropylar end of the embryo sac (Figs. 128, 129, 131, 135). In the middle and chalazal parts of the embryo sac the cytoplasmic strands with endosperm nuclei become placed peripherally close to the embryo sac membrane (Figs. 127–130, 154).

Just before the formation of cell walls, the endosperm nuclei become arranged in the periphery of the embryo sac (Figs. 139–143), especially in the middle and chalazal parts. The nuclei become separated individually by the development of vacuoles between them (Figs. 127, 143, 144, 154). Eventually, the nuclei are separated by the appearance of anticlinal walls without the intervention of mitotic apparatus (Figs. 129, 135, 144, 145). The role of these vacuoles, which always appear between nuclei before the formation of anticlinal walls, is not clear. The development of cell walls not mediated by mitotic spindles has been reported for wheat endosperm (Mares et al. 1975, 1977; Morrison and O'Brien 1976). On the other hand, the formation of anticlinal walls between endosperm nuclei without mitosis has been disputed (Fineran et al. 1982). In the micropylar end of the embryo sac of wild oats, where the endosperm nuclei are embedded in dense cytoplasm, some nuclei do undergo nuclear divisions, and the usual cell plates are formed between nuclei (Figs. 128, 131, 146, 154) unlike in other parts of embryo sac, where the first anticlinal walls are formed independently of mitosis (Figs. 144, 147, 154). Around the proembryo in the micropylar end, the uninucleate protoplasts remain free and independent. The walls between them, if any, are very indistinct. The protoplasts in this region show irregular morphology (Figs. 127, 131, 135).

As a result of the formation of the first anticlinal walls between individual endosperm nuclei, a large number of cylindrical cells appear in the periphery along the embryo sac membrane (Figs. 144, 147). The anticlinal cell walls extend centripetally and often branch. Such branches from adjacent cell walls complete the inner periclinal cell walls. This mode of formation of anticlinal cell walls and the inner periclinal walls is similar to that described for wheat endosperm cells (Morrison and O'Brien 1976). The formation of an outer periclinal cell wall in these cells is also expected. It is not well understood how these outer periclinal cell walls are laid down in the first-formed endosperm cell. The role of the embryo sac membrane in the formation of cells and the outer periclinal walls is not clear.

Despite some variation, the topography of the one-cell thick endosperm layer follows the contour of the embryo sac (Figs. 128–130). Anticlinal divisions of the nuclei in this layer of endosperm, followed by the formation of more anticlinal walls, have not been observed in wild oats. Periclinal divisions are commonly observed in these nuclei producing more cells by normal mitosis. Divisions of this type add more cells, ultimately filling the entire embryo sac, and the identity of the original central cell is completely lost. Because of certain structural restraints, the large amount of endosperm produced gives a characteristic contour that is typical of a caryopsis. In a transverse section the mid-region of a developing grain shows a characteristic distribution of seed parts. The adaxial and abaxial parts of the grain are quite obvious (Figs. 131–134, 136–138). The adaxial part is narrower and confined to the groove region, and the abaxial part lies opposite the groove and is much wider (Figs. 136–138, 150). It also extends to the sides, which are often called the "cheeks," where most endosperm is found in a mature grout (Figs. 137–138).

The formation of the first periclinal wall in the monolayer endosperm results in a two-layered endosperm tissue in which the outer and inner layers of endosperm can be recognized (Figs. 129, 130). The cells of the inner layer are always larger than those of the outer layer. The cells in the outer layer divide again to produce more cells. The resulting cells produced by the most peripheral cells enlarge radially pushing the inner older cells deeper to the centre of the embryo sac. The cell division occurs more frequently on the abaxial side of the developing endosperm and also in the cheek regions of the seed. Often, the most peripheral part of the endosperm on the abaxial side, including the cheek regions, appear "meristematic" (Figs. 133, 134, 150). Most cells of the endosperm in a developing ovule (seed) are derived from the abaxial meristem part of the endosperm. The meristematic activity in the peripheral cells continues to occur until about 15–20 days after anthesis when the outermost cell layer on the abaxial side, and also in the cheek regions of the endosperm, becomes morphologically distinct (Figs. 158). This layer is composed of the most

recently formed cells of the entire endosperm tissue, and it is called the "aleurone layer." In a mature caryopsis, these cells have thicker walls and contain more proteins than the subjacent cells of the endosperm (Figs. 159–160).

In contrast to the first-formed-layer of endosperm cells in the embryo sac, similar cells in the chalazal, or crease region on the adaxial side, show fewer divisions and do not contain meristematic areas (Figs. 138, 150). These cells are somewhat irregular in their morphology and remain protein-rich. The extent of their contribution to endosperm (cells filled with starch) is limited because they soon stop dividing to organize the aleurone layer (Figs. 138, 150). Similarly, those endosperm cells first produced near, and around the proembryo, do not contribute to the endosperm mass. Nevertheless, these cells, like those along the crease or chalaza, remain irregular in shape and rich in proteins and lipids, and differentiate into a layer of aleurone cells (Figs. 128, 129, 131, 135).

The aleurone cells on the abaxial side of the endosperm, including the cheeks, are the youngest, or most recently formed cells (Figs. 150, 155–158). The cells around and on the abaxial side of the embryo are the oldest, or the first formed (Figs. 128, 129, 131, 135, 136). The cells along the crease, or chalaza, are intermediate, and are formed earlier than those on the abaxial side of the endosperm or seed (Figs. 138, 150). Within the massive endosperm tissue, the oldest cells containing starch are found in the middle part of the endosperm, and the youngest are in the periphery. The central part of the endosperm contains large cells with delicate cell-walls, and these often break down, releasing all the contents. During imbibition of seeds the cell obliteration occurs sooner in the central part of the endosperm than in the periphery. The outermost layer of endosperm, the aleurone layer, does not usually contain starch. During the development of endosperm, the new cells are formed in the periphery and the cells situated toward the centre are older. In areas where meristematic activity occurs in the periphery, growth occurs centrifugally. More cells are added on the outside leaving behind the older cells toward the centre (Figs. 156–159).

The endosperm cells are uninucleate, but occasional occurrence of binucleate cells is not uncommon, especially in the middle of the caryopsis. Starch synthesis begins in endosperm tissue after cell-wall formation in it has been completed, and such synthesis proceeds toward the periphery from the centre of the young developing seed. The endosperm cells in the early stages contain nuclei, which seem to be normal (Figs. 145, 149), and which can be recognized by using Feulgen technique (Jensen 1962), although some degree of size difference or hypertrophy can be recognized in the nuclei (Figs. 145, 149, 159). However, in later stages of seed development, the nuclei in the endosperm cells begin to show signs of degeneration or disintegration. In a mature caryopsis, the endosperm nuclei are often represented by "streaks" of DNA when they are stained with basic fuchsin, using the Feulgen technique. A complete absence of such streaks of DNA may be noticed in a few cells.

DEVELOPMENT OF EMBRYO ENVELOPES

As in many grass taxa the embryo of the wild oat is surrounded by a variety of envelopes which I call the embryo envelopes. These envelopes are known to play an important role in the physiology and germination of seeds (Crocker 1906; Werker 1980/81). Some envelopes or covering layers in a mature caryopsis of wild oats have been identified structurally and described in detail (Morrison and Dushnicky 1982). The outermost persistent floral envelopes, such as the lemma and palea, enclose the caryopsis in many grass taxa, and are known to influence caryopsis dormancy and germination directly or indirectly (Crocker 1906; Hsiao 1979; Simpson 1978; Werker 1980/81).

Following double fertilization in the floret of wild oats, many histological and physiological changes occur in the ovule and the ovary. The ovule, within which the embryo and endosperm develop, matures into a seed. The ovary wall enclosing the ovule also undergoes many changes, and persists as a papery or membranous structure, intimately adhered to the developing ovule to form the outermost covering, the pericarp.

The two integuments, each with two-layers (Figs. 161, 167–170), are distinct all around the ovule, except in the adaxial part, which is closely merged with the carpellary tissue. Only the distal parts of the integuments remain distinct without any damage (Fig. 103). Therefore, observations were made on changes in integuments only on the abaxial side of the ovule at various stages of seed development.

Most of the nucellus, except for the nucellar epidermis, will have been completely digested during further growth of the embryo sac after fertilization and development of the endosperm (Figs. 162–165, 170, 172). Meanwhile, the cells of the outer integument elongate considerably and become completely crushed (Figs. 163, 164, 171, 172), as does the inner layer of the inner integument (Figs. 163, 164,

170–173). Thus, in a developing seed, the seed coat is organized basically by the persistent and radially compressed outer layer of the inner integument (Figs. 164, 173, 174). The nucellus is digested or crushed in the seed by the distending endosperm within the embryo sac. In addition to the seed coat formed by the outer layer of the inner integument, the nucellar epidermis and the outermost layer of the endosperm, the aleurone layer, are also modified to form membranes (layers) inner to the seed coat (Figs. 160, 165, 166, 172–175). These two layers and the seed coat are so radially compressed that they appear as either thick or thin cuticular layers (Figs. 173–175). The persistent protein-rich aleurone layer remains distinct and lies inner to the nucellar epidermis.

When histological changes are taking place in different parts of the ovule, the ovule elongates considerably, making the ovary also stretch, mostly in the longitudinal direction. The wall of a young ovary at the distal end is much thicker than the wall at the proximal end (Figs. 102, 103). The ovary cells elongate, especially after fertilization, without much cell division. Consequently, the entire ovary wall becomes thin on its abaxial side. During further development of the seed, the ovary wall is partly obliterated and intimately amalgamated into the external part of the seed. In a mature seed, external to the seed coat the dried ovary wall or pericarp persists (Figs. 165, 166, 174, 175). Thus, the embryo in a mature caryopsis is surrounded by several envelopes, and they occur in the following sequence on the abaxial side of the embryo (equivalent to the adaxial side of caryopsis, or crease side) in a sagittal section: endosperm → aleurone layer → nucellar epidermis → inner integument (outer layer) → remains of pericarp including the inner epidermal layer (Figs. 165, 166, 174, 175). On the adaxial side of the embryo (equivalent to the abaxial side of the caryopsis or opposite the crease side) in the embryo region (not including the cheek sides), the sequence of embryo envelopes from embryo is: aleurone layer → nucellar epidermis → inner integument (outer layer) → remains of pericarp, including the inner epidermal layer. Little or no endosperm is present on the adaxial side of the embryo in a mature caryopsis.

SHEDDING OF THE CARYOPSIS

In about 45 days after anthesis, the caryopses (which are normally covered by lemma and palea) begin to drop from the mature panicles in wild oats. Ordinarily, they are mature and contain well-differentiated embryos. The distal-most ones, both on the main axis and the branches of the panicle, are the first to mature and drop, and the more proximally situated caryopses drop later (Raju and Ramaswamy 1983). Thus, the shattering of caryopses in the entire panicle is continuous, lasting for several days, and it proceeds basipetally from distal ends of both the main axis and the branches of the panicle. In *Avena fatua*, the separation of caryopses occurs above the region of attachment of glumes. Consequently, the dried glumes, which initially covered the entire spikelet, are persistent and remain attached to the peduncle (Fig. 2).

In vascular plants the organs, such as leaves, which are morphologically different yet attached to the stem, are separated by a histologically distinct region or zone. This zone can be identified easily in the early stages of development of these organs. It is often called the "separation or abscission" zone. When the organs are mature, this zone aids in the organic separation causing the dislodging or abscission of the more recently formed organ (the leaf) from the older part (the stem). Similarly, the caryopsis in wild oats is supported by a short or long axis, the rachilla, which is situated above the region of the attachment of the glumes to the peduncle of the spikelet. The caryopsis, being the young and more recently formed organ, gets dislodged from the subtending rachilla which is an older part of the spikelet.

Organ abscission, or separation, is a common phenomenon, especially in temperate plants. Histological and physiological mechanisms associated with the abscission in vascular plants have been described and discussed (Addicott

1982). Abscission of plant parts is a necessary phenomenon for plant survival and regeneration, especially in perennials. The older parts of the plant die and are replaced by the new. In annuals, the process of abscission is important in the survival of species. Individual plants die, and the fruits or seeds must be abscised at appropriate times so that the life cycles of plants can proceed unimpeded. In fact, this mechanism has helped in the periodic shattering of caryopses, and it has made the wild oat species one of the most successful weeds in the prairies (Raju and Ramaswamy 1983).

In wild oats, there are two sites of abscission in the spikelet, one responsible for the separation of the pistil from the floret, the other for the separation of the floret-enclosed-caryopsis (commonly known as caryopsis) from the supporting rachilla. The first type is developed at the base of the ovary, which is connected to the floret axis by provascular strand (Fig. 177). The parenchyma tissue around the provascular strand in the pedicel of a young ovary is solid, with no conspicuous intercellular spaces, until about the time of the development of a mature embryo sac within the ovule. Up to this stage, the tissue at the base of the ovary (in the pedicel) remains brittle because of the lack of vascular differentiation, especially the xylem. Any mishandling or application of physical pressure on the ovary at this stage during pollination or crossing experiments may cause easy detachment of the pistil from rest of the floret. At later stages, however, especially after double fertilization, the provascular tissue becomes extensively differentiated into vascular tissue which affords some fibrous strength to the ovary in that region (Fig. 178). At about the same time or before, the solid parenchymatous tissue around the vascular strand will have changed into spongy or aerenchymatous tissue (arrow in Figs. 178, 179). Although the pedicel contains some spongy tissue, making the region a little weak, the differentiated vascular elements in the provascular strand can provide some strength and rigidity to the pedicel of the ovary, especially after fertilization. In this type of abscission of pistil from the floret, no specific separation zone is observed at any stage of floret differentiation.

The second type of abscission zone in wild oats is developed at the junction of the base of the caryopsis (floret-enclosed-caryopsis), or lemma base, with the distal part of the rachilla, and it facilitates the dislodging of caryopsis from the rachilla. The abscission zone, consisting of nucleated cells, can be recognized at a very early stage when the ovule in the ovary contains the megasporocyte cell; it becomes distinct at about the stage when the mature embryo sac is developed in the ovule. In sagittal section of caryopsis, it is 2–4 cells thick, extending across from abaxial to adaxial side of caryopsis (Figs. 180–185). Although this zone is horizontally placed in a very young spikelet, it later becomes obliquely oriented due to unequal elongation of cells in the rachilla (Figs. 180, 183). This type of deformation in the rachilla can also induce deformation in the floret-enclosed-caryopsis or lemma base, also brought about by unequal cell elongation. Such a deformation, or elongation, of the adaxial part of the rachilla and the abaxial part of the lemma base results in the oblique orientation of the abscission zone, which lies between the two organs (Figs. 180–185). Concurrently, the cells of the abscission zone, which were originally isodiametric in shape, become compressed longitudinally, and the entire zone then appears oblique. Its cells appear small and somewhat radially stretched, and the walls remain thin in contrast to the cells of the base of lemma and the cells of rachilla whose cells become thick-walled. Thus, the thin-walled abscission cell-zone remains sandwiched between the lower rachilla and the upper floret-enclosed-caryopsis, and carries considerable amount of mechanical weakness.

Changes meanwhile occur in the tissues of the rachilla and the base of the floret-enclosed-caryopsis, especially the base of the lemma. After double fertilization, well-developed vascular elements are differentiated in the two strands of provascular tissue, providing mechanical strength to the connecting strands between the caryopsis and the rachilla (Figs. 182, 184, 185). In addition, there are changes in the parenchymatous tissue between and around vascular strands, which becomes modified into spongy or aerenchyma-like tissue enclosing considerable intercellular

spaces, as described earlier by Sargent et al. (1984). The development of such a tissue in the base of the caryopsis and in the rachilla, both organs separated by the abscission zone and still connected by the vascular strands, establishes a mechanical weakness between the two organs in the abscission zone. However, the vascular strands between the two organs, which contain differentiated vascular elements, between the two organs provide a delicate but significant connecting strength, and prevent the caryopsis from shattering, unless some physical pressure is applied to it.

The dislodging of wild oat caryopsis is brought about by a variety of physical factors, such as wind, rain, brushing by animals, etc. One of the effective mechanisms observed in wild oats is the twisting-untwisting contrivance of awns which brings down the caryopsis from the spikelet (Raju 1984; Raju and Barton 1984; Raju and Ramaswamy 1983; Yeung et al. 1987). The awn is essentially composed of a brownish proximal part and an elongated distal awl. The entire awn in a floret of a young developing spikelet, which is part of the lemma, is straight and it is reported to be efficient in photosynthesis in many grass taxa (Grundbacher 1963; McDonough and Gauch 1959; Raju 1984; Rosenquist 1936; Sagromsky 1954). As the caryopsis matures, the straight awn becomes dry, and the brownish proximal part begins to twist on its own axis by losing water; on the other hand, the distal part, or the awl, remains straight. As a result of the twisting of the basal part, the entire awn assumes the geniculate morphology wherein the distal awl appears to be attached perpendicularly to the distal tip of the lower twisted part of the awn (Raju 1984). Such a geniculate morphology of the entire awn is a reliable indication that the caryopsis is fully developed and mature. The proximal part of the awn can again untwist if the moisture supply in the environment is good. Thus, the awn, which is attached to the lemma, can make a periodic twisting and untwisting movement. During this movement of the awn the distal awl may act as a brace and make the caryopsis, including the lemma, turn or twist in the opposite direction. Expending a considerable amount of torque,the awn of the caryopsis can disarticulate at the region of two vascular strands in the abscission zone,

separating the caryopsis from the rachilla. This also is aided by the abscission zone in which the cells show considerable shrinkage and obliteration. The entire caryopsis is dislodged from the subtending rachilla, and drops off the spikelet. The shrinkage and separation of parenchyma cells on either side of the abscission zone in the rachilla and the base of caryopsis occur long before the actual dislodging of caryopsis takes place. The two connecting vascular strands, which are placed oppositely in wild oats, must be broken to dislodge the caryopsis. In natural populations of wild oats, this detachment of the caryopsis can be caused either by physical factors, or by awn movement. It seems, therefore, that the shattering of the caryopsis is mainly a physical phenomenon. In experiments, the caryopsis may be made to remain on the parent plant for a long time by clipping the awl part of the awn (Raju and Ramaswamy 1983).

In a recent paper (Sargent et al. 1984) abscissic acid has been implicated in the promotion of abscission of *Avena fatua* caryopsis. Ultrastructural studies showed that the cells separate in the abscission zone, except in regions where plasmodesmata in walls are densely present. These cells may appear spongy in their early stages. Finally, the areas with plasmodesmatal connections also dissolve, causing abscission, and the caryopsis is shed (Sargent et al. 1984). My study provides additional evidence to indicate that the vascular strands in the abcission zone, which connect the caryopsis and the rachilla, are also important in the dislodging of caryopsis.

MORPHOLOGY AND STRUCTURE OF MATURE CARYOPSIS BEFORE GERMINATION

The dehulled caryopsis of wild oats is morphologically a composite reproductive entity composed of several structural units, all of them essential for the survival of the caryopsis. Fig. 176 gives a topography of these components as seen in sagittal and transverse sections. The two major components are the embryo or germ, and the endosperm or nutritive tissue (Fig. 176). These two components are surrounded by sterile envelopes, commonly referred to as embryo envelopes, which are important in caryopsis protection and germination.

The caryopsis is somewhat spindle-shaped, with distinct proximal and distal ends. The distal part of caryopsis is slightly flattened, and it terminates in two horn-like structures, which are the remains of stylar bases (Fig. 176). The proximal end of the caryopsis is slightly pointed, indicating the position of the primary root tip. Adjacent to this root-tip is a very short persistent projection, often not clearly visible, which represents the remnants of the ovary stalk, the pedicel. On the adaxial side, there is a conspicuous longitudinal groove (furrow), which extends from the proximal end to about one-third of the distance from the distal end where it becomes obscure (Fig. 176). This longitudinal groove is "raphe" or "crease." Morphologically, it represents the remains of the vascular strand of the carpel and the ovule, parts of nucellar and carpellary tissues. These details can be seen in transverse sections (Figs. 176a–j). At certain levels of caryopsis, this region is distinct and often it is dark-brown pigmented, because of cell obliteration (Figs. 186–189); some physiologists call this the "pigment strand" (Morrison and Dushnicky 1982; Zee and O'Brien 1970). Basically, this compound tissue is composed of the non-functional vascular strands, obliterated remains of the

carpellary and nucellar (hypostase) tissues (Figs. 176d–j; 186–189). It does not seem to have any obvious physiological function in a mature caryopsis, at least in wild oats. The laterally bulged part of the caryopsis on either side of the longitudinal groove is termed as the "cheek" and can be seen clearly in transverse sections (Fig. 176d–j).

The ovary wall is several cells thick and part of it is made up of photosynthetic tissue. After fertilization, the ovary wall undergoes considerable histological changes, and most tissues become obliterated to form a membranous pericarp (Fig. 176). The pericarp envelops the entire seed to form the fruit or the caryopsis. The outer epidermal layer of the ovary wall in a mature caryopsis is beset with unicellular forwardly directed hairs or trichomes (Fig. 176). They tend to bend towards the caryopsis wall in water and flare out in a dry environment, showing characteristic hygroscopic behaviour.

On the inner side of the pericarp is a hyaline layer, which is derived from the outer wall of the outer layer of the inner integument; this represents the seed coat. There is one more cuticular layer which is less conspicuous than the seed coat. It lies inner to the seed coat and it is derived from the persistent nucellar epidermis. Such cuticular membranous envelopes occur in other grass taxa (Narayanaswami 1956; Rost 1973; Rost and Lersten 1973). These cuticular membranes, which can be stained positively with Sudan IV, cover both the endosperm and embryo; they also play an important role in germination.

Endosperm

The endosperm in wild oats is a massive nutritive tissue which occupies 80–90% of the total volume of the caryopsis. The *ab initio* free-nuclear endosperm is eventually developed into a cellular, starch-filled storage tissue. There is still a considerable controversy in regard to the way that the cellular morphology is achieved in the endosperm (see Fineran et al. 1982). Nonetheless, the pattern of endosperm development is remarkably similar in all grass taxa, and there are few exceptions.

In about 7–8 days after anthesis, the *ab initio* nuclear endosperm becomes completely cellular. The most peripheral

cells, especially on the abaxial side and around the "cheeks," remain meristematic, as observed in wheat endosperm (Gordon 1922). Continued periclinal divisions in the peripheral cells occur until the aleurone layer is differentiated in the endosperm. The growth of the endosperm tissue is centrifugal, with older starch-filled cells placed in the middle, and the younger cells containing less starch toward the periphery. There seems to be an inverse relationship with reference to protein, the most peripheral layer (aleurone) containing only protein, while the subjacent layers have a decreasing gradient of it. By about 15–16 days after anthesis, when the caryopsis begins to lose water, the frequency of periclinal divisions decreases in the periphery and rest of the regions of the endosperm.

The development of endosperm and the distribution of its starch-filled cells, together with the eventual differentiation of the last layer, the aleurone layer, are similar in detail to those details of wheat and barley endosperm (Evers 1970; Kent and Evers 1961). There are some differences, however. Besides its physiological role, the endosperm tissue is the most important storage tissue on which mankind depends.

Aleurone layer

Rost et al. (1990) have recently reported that in *Briza maxima*, a grass species, the single-layered aleurone is reported to be discontinuous around the embryo. The aleurone layer of wild oats is an important envelope surrounding the endosperm-embryo together in a caryopsis. In fact, this is the only complete envelope. In a recent article, Fulcher (1986) has reviewed the chemical contents of the endosperm and the aleurone layer in cultivated oats, *Avena sativa*. It is taken for granted that a similar chemical composition prevails in the wild oats. Some details of the structure and behaviour of aleurone cells, which were observed in a light microscope, have already been published (Raju 1985, 1986; Raju and Walther 1988).

Irrespective of its origin, topography, and time of differentiation, the aleurone layer is the outermost specialized layer of endosperm tissue within the caryopsis of grasses, including wild oats. Three cell types can be

identified in the aleurone layer of wild oats (Raju and Walther 1988). Most commonly, it is single layered throughout, but it is not unusual to find here and there some two-layered condition. Some aleurone cells in isolated areas may show the two-celled condition, which indicates the occurrence of periclinal divisions. This is, however, the condition that existed in these cells before the caryopsis is dislodged. No divisions occur in the aleurone cells after the caryopsis has been dislodged.

During the transition from the free-nuclear condition to the cellular stage of the endosperm, a large number of endosperm nuclei aggregate around the proembryo, which promptly digests them during its growth. Cell wall formation begins in the endosperm about 4 days after anthesis, separating the free endosperm nuclei into individual compartments or alveoli as described earlier by Mares et al. (1977). Periclinal divisions may occur. The inner cells, if produced, will eventually be digested by the developing embryo. In about 20 days after anthesis, the proembryo will have developed into a morphologically mature embryo with all the identifiable parts in it (Figs. 118–120, 202). The aleurone layer, with its compactly arranged cells, lies intimately on the embryo, extending from the base of the scutellum on its abaxial side, passing over the radicle, almost to the tip of the scutellum on the adaxial side, covering also both the epiblast and the shoot tip of the mature embryo (Fig. 176). The aleurone layer is covered externally by the persistent cuticular nucellar epidermis (Figs. 173–175). The cells of such an aleurone layer covering the embryo belong to the first-formed cell type, and they are designated as "embryo aleurone cells" (Raju 1986; Raju and Walther 1988). It is also important to note that no endosperm with starch-filled cells are produced during the differentiation of embryo aleurone cells, and no endosperm cells lie between the embryo and the embryo aleurone layer (Fig. 176a–c). The embryo aleurone cells are rich in protein and oil (Raju and Walther 1988).

The second cell type comes under the category "groove aleurone cells" which lie on the adaxial side of caryopsis along the crease or groove. These cells, which are derived from the original free-nuclear endosperm, are irregular in

morphology, and contain considerable amounts of proteins and some oil. These cells are developed from free-endosperm nuclei which are arranged around the degenerating antipodal cells within the embryo sac, or the large central cell of the embryo sac. They are found on the adaxial side, far removed from the embryo (Fig. 176), with no apparent direct relationship between them and the embryo. In instances where periclinal division has occurred, the outer cell becomes the aleurone cell, and the inner develops into an endosperm cell, eventually filled with starch. The aleurone layer organization occurs in about 7–8 days after anthesis, when divisions in these cells have ceased. The degenerating antipodals will have completely disappeared meanwhile, making the aleurone layer lie directly on the chalazal nucellar tissue (hypostase). In about 20–22 days after anthesis, the groove aleurone cells become situated between the endosperm and the remains of the hypostase, outside in a mature caryopsis. In a transverse section of the caryopsis aleurone cells of this type are confined to the indented region caused by the nucellar tissue (hypostase) (Fig. 176e–j). The amount of endosperm cells produced during the differentiation of the groove aleurone cells is limited.

The third, and perhaps the most important type of aleurone cells, is the "endosperm aleurone cell" (Fig. 176). In about 7–8 days after anthesis, free-nuclear endosperm becomes completely transformed into cellular endosperm and the embryo- and groove-aleurone layers fully differentiated. Cell divisions begin in the peripheral parts of the cellular endosperm on the entire abaxial side, including the cheeks, of the caryopsis. Periclinal divisions result in the formation of a massive endosperm tissue. The first formed cells remain toward the middle, and the younger meristematic cells toward the periphery, resulting in a centrifugal pattern of growth of endosperm in a caryopsis. Periclinal divisions in the peripheral cells continue until about 20–22 days after anthesis when the endosperm aleurone cells will have differentiated.

Topographically, the endosperm aleurone cells form a single layer and occupy a greater surface area of the caryopsis than the embryo- or groove-aleurone cells.

Although the monolayer of endosperm aleurone cells is common, a few sub-aleurone cells may persist as endosperm aleurone cells without changing into endosperm cells filled with starch. Among the cells derived as a result of mitotic activity, the more centrally situated cells become the endosperm cells each surrounded by a thin cell wall, and in the periphery of the endosperm the endosperm-aleurone cell-walls are thick. Between the endosperm aleurone layer and the centrally placed endosperm cells, there occur intermediate cells whose cell walls show a different degree of thickness. The mitotic divisions in the periphery of the endosperm are normal before differentiation of the endosperm aleurone layer, and the resulting cells are surrounded by thin cellulosic walls.

The cells of the endosperm aleurone layer have normal contents, but they seem to have lost the ability to divide; the same is true when the caryopsis is dislodged from the parent plant. Occasionally, two-celled stages with periclinal walls are observed in the endosperm aleurone layer. These stages present at the time of caryopsis detachment from the spikelet. Basically, the cell walls of endosperm aleurone layer are thin and made up of cellulose. Eventually, abundant adcrusting or incrusting substances, such as hemicelluloses, become associated with the walls, thickening them. So far, no evidence of the occurrence of plasmodesmata in the endosperm aleurone cell walls has been found in a light microscopic study of wild oats. Plasmodesmata are known to occur in the aleurone cell walls of some cereals (Fulcher 1972; Jacobsen et al. 1971; Taiz and Jones 1973). The endosperm aleurone layer, as in the other two types, is intimately associated with the persistent nucellar epidermal membrane. Within the cells of the endosperm aleurone layer are protein bodies called aleurone grains, which show characteristic granular morphology. In the embryo and groove aleurone cells, on the other hand, similar grains appear to be absent, or, if present, they are not obvious in the light microscope.

The behaviour of isolated aleurone cells, especially the endosperm aleurone cells, is quite interesting. These cells show some fundamental structural changes when they are

subjected to hydration or desiccation. These changes occur in response to the presence or absence of water only (Raju 1985, 1986; Raju and Walther 1988). When these cells are dried, both the protoplast and the cell wall shrink by losing water, and within the cells appear characteristic spiny vesicles, extending from the protoplast to the cell wall (Raju 1986). In microtome sections, these dessicated cells show vesicles, vacuoles or cavities of different size (Raju and Walther 1988). The structures have been variously described (see Bhatnagar and Sawhney 1981; Jacobsen et al. 1971). These vesicles in the desiccated cells disappear immediately after hydration, and both the cell wall and the protoplast of these cells expand (Raju 1986). The protoplast does not fully expand because the cell wall expands earlier and exerts enough force to prevent the protoplast from expanding maximally. The walls of these endosperm aleurone cells contain, besides cellulose, abundant hemicelluloses which presumably help in the contraction and expansion of cell walls. The expansion process may also be implicated in the long water-holding ability of the aleurone cell in the caryopsis. The proteins and some carbohydrates in the protoplast may also allow the protoplast to retain water. These features, which include expansion and contraction of the protoplast and the cell wall due to hydration and desiccation respectively, are seen neither in the embryo aleurone cells nor in most of the groove aleurone cells (Raju 1986; Raju and Walther 1988).

The aleurone layer is an important envelope around the wild oat embryo and it is structurally heterogenous, consisting of at least three cell types, as described earlier. Whether these types are also differ functionally needs to be determined. In their work on barley grain Mann and Harlan (1915) suggested a possible protective function for the aleurone layer. It is a very resistent tissue protecting the kernels from microbial attack. In wheat kernels, the aleurone layer surrounding the embryo may have a role in water uptake (Bradbury et al. 1956a, b, c). The most commonly accepted idea is that the aleurone cells produce enzymes which are important in the endosperm breakdown, and in subsequent embryo growth in wild oats and other cereals

(Bewley and Black 1978; Simpson 1978). Simpson (1978) suggested that both the aleurone and the endosperm have an important role in sustaining early seedling growth.

Some studies relating to the histological behaviour of the aleurone cells indicate that the aleurone layer may act as an important recalcitrant barrier, especially in a dry caryopsis, protecting the endosperm and embryo in wild oats. It is also known that any slight injury to the aleurone layer in an intact seed can release an embryo from dormancy or promote germination (Hay 1962; Hsaio et al. 1983; Nair and Sahadevan 1962; Raju and Tom 1986; Raju et al. 1986, 1988). The aleurone layer may be important in regulating water balance both in dormancy and in the germination of wild oat caryopsis. The occurrence of such an important aleurone envelope in two of the largest families, the Gramineae and the Compositae, may also have a phylogenetic and taxonomic significance which needs to be explored.

Mature embryo

Following the process of double fertilization, the zygote undergoes a predetermined sequence of cell division to form a massive proembryo in which the sites of early initiation of embryo parts are determined. More cell divisions and differentiation in the proembryo result in a mature embryo of the grass type in which the fundamental embryo parts become established. Concomitant with the development of the embryo, the primary endosperm nucleus divides many times to form initially a nuclear type of endosperm, which is transformed finally into a massive cellular endosperm. In the Gramineae, including wild oats, the development of the endosperm precedes that of the embryo. In most angiosperm taxa, the embryo is generally buried in the endosperm. In the caryopsis of the Gramineae the embryo is uniquely situated external to the massive endosperm tissue, and it is still covered by the aleurone layer, which is developmentally a derivative of endosperm. It is not clear at present whether this type of disposition of the embryo in relation to the endosperm tissue has any physiological and/or evolutionary significance. However, it does have a taxonomic value; in the

caryopsis, the embryo is always situated outside the endosperm, and can be distinguished from others which have their embryos embedded in the endosperm.

The mature embryo occupies about 10 percent of the total volume of the caryopsis in wild oats. The grass embryo is composed of certain fundamental parts, some of them not seen elsewhere. Their homology, analogy, etc., have been discussed (Brown 1959, 1960, 1965; Natesh and Rau 1984). The basic parts of the embryo whose morphological interpretations have been controversial are the scutellum, the coleoptile, the epiblast, the coleorhiza, and the mesocotyl. The morphology of these parts is summarized by Brown (1960, 1965), Natesh and Rau (1984) and Negbi and Koller (1962).

Development of some embryo parts

During its development, the embryo goes through several stages carrying with it several histological changes. The zygote produces a large proembryonic tissue in which many embryo parts are differentiated. Each of these parts initiated in definite sites appears later as a recognizable part in the mature embryo in a caryopsis. After the sites in the proembryo are used up in the formation of embryo parts, it is important to note that the mature embryo with its parts is still associated with unused parts of the proembryonic tissue. These unused portions of the proembryo may remain the same, or they may become modified in some way, such as the coleorhiza in the embryo.

In about 5–6 days after anthesis the proembryo becomes a massive tissue in which internal and external differentiation may be observed. It is top-shaped in the surface view (Fig. 190a, b). On the adaxial side of the proembryo (or embryo), a small protuberbance of the "coleoptile bud" appears rupturing the proembryonic tissue. As a result of this lateral protrusion on the adaxial side, a circular rim or coleoptile rim or scar is formed (Fig. 190a–e) surrounding the coleoptile bud in which a small coleoptile pore is organized (Fig. 190d–f). On the abaxial side there is a flat, somewhat rounded pad representing the scutellar initial (Fig. 190b–d). This undergoes considerable growth, resulting in a mature

scutellum (Fig. 190e–h). The inverted cone-like structure, proximally situated, is the coleorhiza, a proembryonic tissue covering the internally situated primary root (Fig. 190f).

Internally, the proembryonic tissue will have differentiated the shoot and root apical meristems establishing polarity (Figs. 122, 190a). The scutellum is quite vigorous in its growth and, in about 8 to 10 days after anthesis, it develops into a shield-like organ (Fig. 190b–d). The proximal part of the embryo is actually the portion of the proembryo which eventually becomes the coleorhiza. At the extreme proximal end of the coleorhiza is the suspensor, which is still a part of the embryo (Figs. 117, 120). The circular or coleoptile rim, a part of the proembryo, surrounds the coleoptile bud, and is continuous proximally with the coleorhiza (Fig. 190c–e). The portion of the coleoptile rim in contact with the coleorhiza produces on the adaxial side a scale-like thick structure, the epiblast (Figs. 117p, 190f). It elongates to form the membranous epiblast without much cell division (Fig. 190f). The mature epiblast in wild oats is morphologically quite variable (Raju et al. 1988b). Considerable elongation of both the scutellum and the embryo axis occurs and, consequently, the contour of the coleoptile rim also changes to an oblong rim in a sagittal view. By meristematic activity of cells along the rim, this produces a membranous extension or flap partly covering the embryo axis on the adaxial ridge (Fig. 190f). In a sagittal median section, it appears as an outgrowth called the adaxial or ventral scale on the adaxial side (Figs. 119, 125, 176). Opposite to it, on the same side the coleoptile rim associated with the coleorhiza, is the epiblast (Fig. 190f). On the abaxial side of the embryo, a central longitudinal abaxial ridge is formed (Fig. 190g, h). There are detailed, well illustrated accounts of the embryo and embryo parts of many grasses, especially the scutellum and the epiblast (Bruns 1892; Nörner 1881). A similar and extensive taxonomic survey of embryos in grass taxa was made by Kinges (1961).

Anatomy of the Mature Embryo

The embryo of wild oats at the time of germination is a dorsiventral structure with all the fundamental embryo parts

fully differentiated. It is situated laterally to the endosperm, with only the scutellum in contact with the massive endosperm (Fig. 176). The tissue relationships between the endosperm and embryo are indicated in the long section and several transverse serial sections taken at selected levels of the caryopsis in Fig. 176. Only a few levels are shown in the illustration (Fig. 176a–j).

The embryo structure is anatomically simple; with the exception of the scutellum, it is composed solely of provascular tissue, especially in its distal parts, where a few xylem and phloem elements may be found (Raju et al. 1986). The embryo axis itself is a cylindrical structure, but the associated scutellum shows a dorsiventral morphology (Fig. 191). On the adaxial side, the embryo axis is partly covered by the adaxial ridge (Fig. 191), which in some instances almost completely covers the embryo axis. On the abaxial side of scutellum, there is a small bulge or mound which represents the abaxial side of the coleoptile bud within the embryo (Fig. 191a). Extending from it, almost to the tip of the scutellum, is a longitudinally placed adaxial ridge, which indicates the underlying provascular tissue (Fig. 191a).

Figs. 191, 191a provide a general view of the adaxial and abaxial sides of the dorsiventral mature embryo before caryopsis germination. The transverse sections taken at different levels of mature embryo give a general picture of the structure and morphology of the embryo. Although there are many transverse sections shown (A–H, J–W), only a few levels are indicated in the embryo surface view (Fig. 191). The transverse sections of the mature embryo (Figs. 191A–H, J–W) give a general idea of the disposition of provascular strands in the mature embryo.

At the most proximal level only the coleorhiza is observed (Fig. 191W). A little higher toward the coleoptile, the coleorhiza appears as a thick envelope enclosing the distal part of the primary root (Fig. 191V). Further back, at about the level of the scutellar node, the organization of the embryo is rather complicated, mainly because there is no clear distinction between the proembryonic tissue and the newly formed embryonic parts. The coleorhiza, scutellum, proximal parts of the root, and the epiblast are all amalgamated. The

scutellum appears as a dorsiventral structure attached basally to the coleorhiza on the abaxial side, and the epiblast to the proximal part of the coleorhiza on the adaxial side. A little higher up, the small epiblast becomes separated from rest of the complex tissue (Fig. 191R, S) and the central core of the primary root is clear (Fig. 191T, U). Fig. 191Q and R are just above the scutellar node where provascular strands (traces or bundles) of scutellum and first leaf appear, both arising at the scutellar node. At the coleoptile node in the central core appear three strands arranged in a vertical row (Fig. 191P); two of them belong to scutellum, the third to the first leaf. In the coleoptile node (Fig. 191O), the provascular strand of the scutellum branches to form two coleoptile strands, each placed opposite to the other within the coleoptile. At about the same level, the first leaf strand also branches to form more bundles (Fig. 191K–O) and the coleoptile bundles become distinct. The new second leaf primoridium also appears almost opposite the first leaf, and the shoot apex is also distinct at this level (Fig. 191J). Further towards the distal end, the scutellum becomes wider, and the longitudinal abaxial ridge becomes prominent. The scutellum itself becomes narrower.

ANATOMY OF THE POST-SEMINAL EMBRYO (YOUNG SEEDLING)

Soon after caryopsis (Fig. 192) germination, the emerged embryo (seedling) may exhibit morphological variability because of a number of environmental factors (Figs. 193, 195). One important factor in wild oats, and probably in other grasses, is the depth at which the caryopses are buried in the soil. Following germination the embryos emerge from caryopses, and the seedlings come up to ground level. During wild oat caryopsis germination, besides the growth observed in the shoot and root, the "mesocotyl," the internode between the coleoptilar and the scutellar nodes, elongates significantly, as it does also in cultivated oats, wild rice, and maize (Bonnett 1961; Boyd and Avery 1936; Hanten et al. 1980; Kaltofen et al. 1984). Similar changes occur in the scutellum, which becomes an elongated absorbing organ within the grass caryopsis (Fig. 194) (Negbi 1984; Negbi and Sargent 1986; Raju et al. 1986, 1988a, b). Some, however, consider the cotyledon or scutellum as haustorial in nature (Bewley and Black 1978), although it is more an absorbing organ.

The mature embryo is composed of all the embryo parts, as is the case in any other grass embryo within which the provascular tissue is already differentiated (Fig. 196). No fully differentiated xylem strands are observed in the entire embryo, except in the scutellum where a few scattered elements may be found (Raju et al. 1986). The embryo axis (the region between the shoot apex and the scutellar node) contains cortical cells filled with starch, especially on the scutellum side. Similar starch-filled cells also occur just below the scutellar node (base of primary root). Immediately after the emergence of the primary root, the cells in the abaxial part of the embryo axis (marked in asterisks in Figs. 196–201) begin to elongate lifting the shoot tip distally. This

elongation of cells occurs in the region where the coleoptile strand is connected to the scutellar strand (Figs. 196, 197). Because of the elongation of this part of the embryo axis (indicated by asterisks) the provascular tissue is pushed up, and the provascular tissue of the scutellum becomes inverted (Fig. 198). Consequently, the entire scutellar provascular strand shows a double hairpin bend, one near the coleoptile strand, the other at the junction of scutellar base and embryo axis (Fig. 199–201). To keep up with the increasing length of the embryo axis on the abaxial side, the cells on the adaxial side of the embryo axis between the coleoptile node and the epiblast also elongate. This elongated part of the embryo axis is then the "mesocotyl" extending from the base of the primary root (scutellar node) to the base of coleoptile node where the first leaf is also situated (Fig. 200).

The elongation of the part of the embryo axis (or the mesocotyl) depends on the depth at which the caryopsis is buried. Although the elongation of the mesocotyl is somewhat slow, the caryopses can germinate at greater depths and the seedlings can come up to ground level (Fig. 203). The increased length of the seedling is due mainly to the elongation of the mesocotyl (Figs. 199–201, 203). The internodes, such as the one between the first and second leaves, the second and third leaves, etc., also contribute to the length of the seedling shoots. The elongation of the mesocotyl may be considerably reduced if vascular differentiation occurs in it very early. As elongation of mesocotyl, at least in the early stage of seedling development, is not synchronous with vascular differentiation, it is not unusual to find discontinuous xylem and phloem strands in the embryo axis. Similarly, on the adaxial side of the mesocotyl, the vascular strand of the first leaf also elongates; it contains discontinuous xylem and phloem strands, at least in the early stages of mesocotyl elongation. Eventually, a massive vascular tissue appears in the mesocotyl. It results from the amalgamation of the lower part of the scutellar strand (erect strand extending from the scutellar node to the region where coleoptile strand branches), the upper part of the inverted scutellar strand extending backwards from the coleoptile branch to the scutellar base (equivalent to nodal

region), and the basal part of the vascular strand of the first leaf (Figs. 200, 201). The mesocotyl, and the pattern of vasculature associated with it, seem to have some taxonomic value. The disposition of vascular strands in the hypocotyl (mesocotyl) and the degree of elongation of the mesocotyl have been used to separate different taxa of grasses by Reeder (1957).

The vascular strand of the scutellum begins at the scutellar node, extending into the scutellum through the coleoptile which is, in fact, a part of the scutellum. The first leaf is situated opposite the scutellum and at the coleoptile level. However, the vascular strands of both scutellum and the first leaf proximally end in the scutellar node or at the junction of the root base and the scutellar base. Excessive growth in the cells on the abaxial side of the embryo axis in the region below the coleoptile and on the adaxial side, below the first leaf, results in an elongated region of the embryo axis. This is the "mesocotyl," in my study an equivalent to the term "hypocotyl," which is commonly used for dicots.

After the wild oat caryopses have dropped to the ground, they often slip through crevices to deeper levels, or get buried deeper in the ground during soil drift, etc. An experiment was conducted to simulate this situation, to determine the ability of seedlings to come up to ground level, and to observe morphological changes, if any, in the seedlings. Non-dormant caryopses (CS 40) of wild oats were used in the experiment to ensure that they all showed maximum viability and germination. The dehulled caryopses were buried at different depths in plastic pots containing garden soil. All caryopses germinated at all depths, and emerged above soil (Fig. 203). The pattern of germination and seedling growth showed a positive correlation between the emergence of seedlings above soil and the time taken for it (inset in Fig. 203). Immediately after germination the mesocotyl (hypocotyl) elongated and pushed up the coleoptile node and the epicotyl. The mesocotyl elongation was considerable and at the summit of the mesocotyl, i.e., the coleoptile node, the epicotyl contained several root and leaf primordia. The mesocotyl elongation appeared to be limited (Fig. 203) and the rest of the elongation to make the epicotyl reach the soil surface was

achieved by the elongation of the coleoptile and the base of the first leaf (second cotyledon, as interpreted here). Although the seedling elongated considerably to reach the ground surface, the epicotyl was situated still at the tip of the mesocotyl. The membranous, tubular coleoptile elongated, protecting the enclosed elongating leaves and the epicotyl. This pattern of uplifting is characteristic, especially of seedlings emerging from greater depths. The distal parts of the leaves, which may still be enclosed in the coleoptile, become chlorophyllous after reaching ground level. Thus, the coleoptile is presumably an important structure protecting the epicotyl at the coleoptile node and the elongating leaves until they reach ground level. In some instances, the extent of coleoptile elongation appears limited (Fig. 203) when the leaves inside have penetrated the distal part of the coleoptile to reach the soil surface.

Assuming that light penetrates different depths of soil where caryopses lie buried, more light is available at shallower levels than at deeper levels. The extent of the mesocotyl's elongation is considerably less at shallower levels than at greater depths, indicating that light has an inhibitory effect in cultivated oats, as demonstrated by Goodwin (1941). This inhibition of mesocotyl length by light may be due primarily to low humidity in the environment (Mer 1951, 1953). Therefore, the depressed growth of the wild oat mesocotyl at shallower levels (Fig. 203) may be due to low relative humidity, a condition probably caused by high light intensity.

The coleoptile itself does not elevate the seedling to the soil surface by itself. It is the mesocotyl which pushes the seedling toward ground level above, at least in the early stages of seedling growth in the soil.

The extension of the mesocotyl is somewhat limited (Fig. 203). The internodes above the first leaf node may elongate considerably, supplementing the elongation of the mesocotyl, to make the seedling shoot reach the soil surface. The epicotyl, with its very short internodes, remains situated at the distal end of the mesocotyl (or coleoptile node), and begins to elongate after some leaves have come up to the soil surface.

The scutellum of the embryo, which remains within the caryopsis as a suctorial organ, elongates soon after germination. It becomes active by producing papillae (Rao and Raju 1985; Raju et al. 1986; Raju et al. 1988a). The increase in the length of the scutellum is maximal immediately after caryopsis germination, and it remains about the same within the caryopsis at all depths. However, the scutellum produces papillae profusely to digest and absorb the nutrients of the endosperm in the caryopsis. After caryopses germination, the seedlings emerge from greater depths. These caryopses still contain large amounts of endosperm, indicating that seedlings during their growth use endosperm very sparingly.

MORPHOLOGY OF THE WILD-OAT (GRASS) EMBRYO PARTS

There is considerable controversy over the interpretation of the morphology of the grass embryo and its parts. A mature grass embryo has a central axis, and it is associated with some embryo parts, most of them common in all grass embryos, including wild oats. Homologies of some of the embryo parts have been described and discussed in a few papers (Brown 1960, 1965; Clifford 1961; Guignard 1961; Negbi and Koller 1962; Natesh and Rau 1984; Sendulsky et al. 1986). My definitions and interpretations are based on observations made on embryos of *Avena fatua*, the wild oat. Homologies of these different organs of the wild-oat embryo are given in Table 4.

Scutellum

The scutellum is considered as the first cotyledon and is derived entirely from the proembryonic tissue. The scutellum is situated laterally to the shoot apex. It is functionally a suctorial organ transporting nutrients from endosperm to embryo. It is not a haustorium in a morphological sense. The central vascular strand of the scutellum is proximally connected to the proximal end of the primary root (scutellar node).

Coleoptile

The coleoptile is a part of the scutellum and, therefore, is a part of the first cotyledon. With some reservations it can be considered to be equivalent to the basal sheath of a leaf. It receives two vascular strands as branches from the scutellar strand, and each lies at right angles to the scutellar bundle. The coleoptile bundles run longitudinally independently and terminate blindly as proliferated strands at the distal end of the coleoptile. Functionally the coleoptile forms a tight cylindrical cap protecting the first leaf and the shoot apex. It

also provides adequate humidity or moisture to the developing shoot apex within.

As in ordinary photosynthetic leaves, the stomates of different morphology are distributed on the coleoptile. The functioning of these stomates in photosynthesis is not clear at present (O'Brien 1966; O'Brien and Thimann 1965, 1966).

First Leaf

This leaf is interpreted in my study as being equivalent to the second cotyledon. The primordium of this leaf is derived from the proembryonic tissue. The first leaf is situated opposite the scutellum at the level of the coleoptile base. The vascular strand from the leaf is directly connected to the scutellar node, and is similar to that of the scutellum. Functionally, the first leaf is photosynthetic. Thus, in wild oats, and possibly in other grasses, there is cotyledonary dimorphism. One cotyledon (the scutellum) remains within the caryopsis as a suctorial organ, while the second cotyledon (first leaf) is modified to form the first true photosynthetic leaf. Such dimorphism of cotyledons, one suctorial and the other photosynthetic, is seen in some primitive Piperales and the Liliales (Burger 1977, 1981; Bewley and Black 1978; Eames 1961; Hill 1906, 1907).

Epiblast

It is a common membranous flap developed on the adaxial side of the embryo and forms a part of the proembryo similar to the coleorhiza. The coleoptile bud enlarges, and ruptures the proembryonic tissue leaving a round or oval scar or rim around the coleoptile bud in the proembryonic tissue. This rim, due to "wound healing process" forms a narrow regenerated ridge all around by cell division and enlargement. It forms a thin flap, or adaxial ridge, partly covering the underlying embryo axis (Figs. 190, 191). The proximal part of the coleorhiza (proximal part of the rim) on the adaxial side of the embryo proliferates to form this flap, which is equivalent to the ventral scale on the scutellum (Figs. 176, 190, 191). Thus, the epiblast is a newly proliferated tissue at the base of the coleorhiza, and is still derived from proembryonic tissue. It does show characteristic morphology or shape, different from other embryo parts, and

it is used as a taxonomic character in the identification of certain grass taxa (Baum 1977). Its morphology is rather variable, and is sensitive to external humidity (Raju et al. 1988b); often in high humidity characteristic unicellular hairs, that are common to coleorhiza also, are produced.

Coleorhiza

It is undoubtedly a distinct structure entirely derived from the proembryonic tissue. It represents the remains of the proximal part of proembryo and the entire suspensor. The coleorhiza forms a conical cap around the developing primary root. Its cells often contain starch, and they do not divide, but do elongate enormously. When the primary root begins to elongate the coleorhiza also becomes stretched and distinct. Under certain conditions, the coleorhiza can elongate without being pushed by the primary root inside (Raju et al. 1988b). Ordinarily, the root elongates, rupturing the coleorhiza during caryopsis germination. In some instances the coleorhiza can precociously elongate and push through the embryo envelopes during germination, probably facilitating root emergence. Functionally, the coleorhiza protects the primary root and keeps the young primary root inside moist.

Mesocotyl

The mesocotyl is the embryo axis, which is derived from the proembryonic tissue and the primary embryonic meristems. It is morphologically equivalent to the hypocotyl of seedlings. It represents the first internode (region or structure) which extends from the proximal part of the primary root to the base of coleoptile. It is also the part situated between the two poles, the root and shoot apices in a young embryo-axis. Functionally, it probably plays an important role as a liaison tissue receiving nutrients from the scutellum and transferring them to root and shoot apices. It is also important in bringing the epicotyl to the ground surface from greater depths after caryopsis germination.

GERMINATION

The embryo in angiosperms is situated within a seed (caryopsis in grasses) which is a product of double fertilization. The seed, a well-organized unit of reproduction, is produced as an important stage in the life cycle of an angiosperm and frequently undergoes a period of dormancy or rest. The extent or the degree of dormancy may vary considerably in different taxa. In the event of favourable conditions, the embryo root emerges visibly from the seed, and this process is called "germination." The phenomenon of seed germination has been studied extensively for the last many years, both physiologically and biochemically, and enormous numbers of publications have accumulated. According to one report 53% of the total number of papers published on caryopses are related to physiology and biochemistry (Sendulsky et al. 1986) signifying the importance of seed research. The two volumes on the physiology and biochemistry of seeds by Bewley and Black (1978, 1982), and the recent book by Simpson (1990), form an excellent source of information for the study of many aspects of seed dormancy and germination. In addition, there are some reviews which provide specific information on these aspects. Simpson (1988) has also published an annotated list of papers with about 900 publications on wild oats (*Avena fatua* L.) alone.

In many investigated taxa, it is common to find that freshly harvested seeds do not readily germinate unless they are subjected to a period of after-ripening. This phenomenon of delayed germination is often referred to as "dormancy." The many types of dormancy manifested in seeds and fruits have been investigated extensively (see Bewley and Black 1978, 1982; Khan 1977; Simpson 1978, 1990). Most investigations have been on cereal or grass seeds, mainly because the endosperm, which makes up the major part of

the caryopsis, has two morphologically distinguishable cell types. The cells, containing abundant starch, form the major part of the endosperm which supplies the embryo with nutrients. The second type, which is present in most grass caryopses, consists of a layer of cells containing no "starch" but abundant proteins instead. These cells are known to contain special protein granules, the aleurone grains. A layer of such cells envelopes both the endosperm and embryo, at least in the wild oat caryopsis (Raju and Walther 1988), and it is called the aleurone layer, which in ontogeny is similar to endosperm.

It is generally believed that the aleurone cells contain abundant hydrolytic enzymes, which are released into the endosperm during caryopsis hydration or imbibition. Such enzymes are known to breakdown the endosperm starch into simple sugars, which eventually are made available to the embryo for its growth (Bewley and Black 1978; Jacobsen 1984). A modified version of the same process is often provided in the literature suggesting that the embryo produces a substance 'X' or gibberellin (GA_3 and GA_1) which stimulates the aleurone cells to produce required enzymes (α–amylase, etc.). These enzymes are somehow released into the endosperm for action (Bewley and Black 1978; Jacobsen 1984; Schander 1934). The degradative products of endosperm somehow become available to the scutellum which absorbs and transports them to the embryo axis. It is also reported that the enzymes, such as α–amylase, are produced directly by the scutellum of the embryo (Okamoto and Akazawa 1979). Whatever the source of primary production of enzymes is, it seems obvious that the breakdown of endosperm is a post-germination process (Chen and Varner 1970; Chen and Chang 1972).

Of late, the idea of "coat-imposed dormancy" (Crocker 1906; Crocker and Barton 1953; Wareing 1965) has been revived, and the relation between seed structure and dormancy has been reviewed extensively (Bewley and Black 1982; Simpson 1978, 1990; Werker 1980/81). Very appropriately called "embryo envelopes" (Werker 1980/81), many such structural envelopes surround the embryo. Although lemma and palea are persistent floral envelopes

present around the embryo, they do not have a direct marked effect on breaking caryopsis dormancy or germination. However, the remaining envelopes, such as endosperm, aleurone, seed coat, and pericarp, are closer to the embryo and do have some role to play in the dormancy or delayed germination of caryopsis. The occurrence of coat-imposed dormancy in *Avena fatua* caryopses has been attributed to some persistent floral parts, such as palea, lemma and pericarp (Bewley and Black 1982).

Atwood (1914) first demonstrated that pricking the dehulled caryopses of wild oats greatly increased germination. The envelopes presumably act as barriers against oxygen uptake (Atwood 1914). Similarly, Johnson (1935) showed that caryopsis germination can be promoted by mechanically breaking the caryopsis, or producing a similar effect by other caustic chemical agents. Hay (1962) repeated similar experiments, and provided a different interpretation by suggesting that lack of oxygen did not prevent the germination of pricked caryopsis. Nair and Sahadevan (1962) found that the rice caryopses germinated better when the bran was removed, implicating an inhibitory effect of bran on caryopsis germination. Recently, Weidner (1988) has demonstrated that the germination inhibition of triticale caryopsis can greatly be reduced by removing the embryo envelopes, such as testa, pericarp and endosperm.

The embryo of wild oats is covered by several envelopes which can be carefully removed in sequence, so the effects of each can be determined (Raju and Tom 1986). Germination can be increased by removing the aleurone layer envelope from the caryopsis (Raju and Tom 1986). The other envelopes, such as the pericarp, and seed coat, which lie external to the aleurone layer do not seem to have any effect on germination. If the aleurone layer is retained, caryopsis germination is greatly inhibited, confirming the earlier report on rice by Nair and Sahadevan (1962). Thus, evidence is available to suggest that there exists a coat-imposed (aleurone layer) dormancy in wild oats.

Results of a comparative study on the effects of mechanical injury on water uptake and germination in different genetic strains of wild-oat caryopses indicate that

the embryo envelopes, especially the aleurone layer and its intimately associated nucellar membrane, have a role in preventing caryopses germination (Hsiao 1987; Hsiao and McIntyre 1988; Hsiao et al. 1983; Raju and Tom 1986; Raju et al. 1986, 1988b). Mechanical injury, such as cutting the caryopsis or incising or abrading embryo envelopes, brings about a significant increase not only in caryopsis germination, but also a significant increase in embryo water content. This suggests that the embryo envelopes act as barriers against adequate water transport into the embryo (Hsiao 1987; Hsiao et al. 1983; McIntyre and Hsiao 1985; Raju et al. 1986, 1988b). When the embryos are completely freed from rest of the parts of the caryopses, both dormant and nondormant, and placed on a wet filter paper, they do grow. It seems, therefore, that the embryo envelopes play an important role in regulating the uptake of water by the embryo in an intact caryopsis of wild oats (Raju et al. 1988a).

While describing different mechanisms of seed dormancy in grasses, Simpson (1990) has developed a comprehensible model system to explain the induction and breakage of dormancy in seeds. He recognizes the occurrence of specific functional units, the holons, which promote seed germination. To make the holons functional, many external factors are required, singly or synergistically in unison, to reduce the diffuse asynchronous steps of metabolic activity to an organized synchronous state, leading to a specific achievement of a developmental change, such as seed germination. This hypothesis is interesting and needs to be tested further with more experiments. One external factor often recognized is water. It has the unique ability to harmonize many metabolic reactions, which bring about morphological and developmental changes (McIntyre 1987). There is considerable evidence to suggest that the embryo water-content forms a critical threshold, and that an increase of water content can promote radicle emergence or germination of the wild oat caryopsis (McIntyre and Hsiao 1985; Raju et al. 1988a). The embryo may be the site of holons in a dormant seed, and when these holons are harmonized by the exogenously supplied water, the seed is released from dormancy.

CONCLUSIONS AND COMMENTS

Tables 5 and 6 list some important chronological events with respect to the vegetative and reproductive phases of the life cycle of wild oats. This book is involved mostly in the description of the reproductive phase of the wild oat. Although the details provided are primarily for wild oats, the same details, in most instances, may apply to other grasses as well. "Classically, the terms raceme, spike, and panicle are used to describe the basic types of grass inflorescence. Compound raceme, compound spike, and compound panicle are terms that have been applied to specialized forms. The use of this terminology is unfortunate, as the determinate pattern of growth is cymose rather than racemose. Both spike and panicle are generally defined as variations of the raceme, and by exact definition these also should have the indeterminate flowering of the true raceme. In the absence of satisfactory alternative terminology, grass inflorescences will be classified as panicle, raceme and spike" (Gould 1968).

Developmental studies in the wild oat indicate that the inflorescence is a panicle (Gould 1968), and that it is determinate. The pattern of development of the panicle is already determined, and the primordia of spikelets are formed well before the emergence of the inflorescence through the flag-leaf sheath. The first formed or the oldest spikelet is the distal-most on the main axis of the emerged panicle.

It is also unfortunate that the units of the determinate panicle are called the "spikelets" (for definition see Gould 1968). I have deviated from the generally accepted definition that the unit of a panicle is a spikelet. I have provided anatomical evidence to show that it is a "cymelet" and not a "spikelet." If there are two or more florets in a spikelet, this inflorescence appears to follow a spike definition (see Gould 1968). In my book, the florets are interpreted as terminal

and, consequently, if there are many florets, the inflorescence appears more like a "scorpioid cyme" (Lawrence 1951) rather than a spike. Therefore, the term "cymelet" seems more appropriate to me. However, the term "spikelet" is so deeply embedded in the literature that it may be difficult to replace it with the term "cymelet" at once.

The acceptance of the terminologies "determinate panicle" and "cymelet" is of considerable importance with respect to determining the caryopses' maturity and germination. For example, in the determinate panicle of wild oats, the distally placed spikelets, both on the main axis and on the lateral branches, mature earlier, their caryopses shatter earlier, and caryopses germination is better. The spikelets in the more proximal regions of the panicle mature slowly, and the caryopses, which have delayed shattering, germinate poorly. However, in an individual spikelet (cymelet), irrespective of its position on the panicle, the most basally situated, or the first-formed caryopsis, which matures earlier, is larger and germinates better than the distally placed caryopses. This pattern may not be present in seeds or fruits developed in a normal spicate inflorescence (Lawrence 1951). Often, such first-formed, or primary, caryopsis in wild oats may remain on the spikelet longer, and mature and germinate better than the later-formed second, or secondary, caryopsis in the same spikelet that drops much earlier.

My interpretation that the unit of the inflorescence of wild oats is morphologically a cymelet, differs from the hitherto held view that it is a spike; some botanists may be critical of my interpretation. Therefore, it is necessary and important that more taxa of grasses, and possibly other closely related monocots, be investigated to support or disprove my interpretation.

The "seed" represents a modified stage in the life cycle of all higher vascular plants. The seed habit itself is ancient and had its origin late in the Devonian (Steeves 1983). With respect to the structure and organization, the seed of angiosperms is distinct from that of other groups of plants, extant or extinct. In all sexually reproducing angiosperms, both monocots and dicots, the seed can be considered as a product of a morphological, cytological, and genetical event

called "double fertilization," a unique process that can be regarded as a "compelling testimony to the monophyletic origin of angiosperms" (Steeves 1983). Concomitant with this double fertilization, there is also a unique organization in the seed. For example, in the annual wild oat taxon, the seed is the only reproductive propagule. In this seed (caryopsis), as in others, there are three tissue units which are functionally integrated. The embryo forms a distinct unit, eventually producing a complete plant. The endosperm tissue supplies nutrition to the developing embryo. The third type is more heterogeneous and represents the remains of the parental tissue, which becomes variously modified to become protective embryo envelopes. Thus, in a caryopsis, the embryo is intimately associated with the nutritive endosperm, and both these units are surrounded by protective envelopes, indicative of biological organization.

The plant sexual life-cycle is composed of a series of uninterrupted developmental stages some of them gametophytic and others sporophytic. In seed plants, where the dominant plant body is the sporophyte, the most important developmentally arrested stage is the diploid seed. By contrast, in the dominant gametophytic multicellular algae, the arrested stage is usually the haploid asexual spore (Bold and Wynne 1978). Both the seed and the asexual spore have the potential to develop into a mature sporophyte and a mature gametophyte respectively. In such stages or structures the expected growth does not proceed, because of a variety of factors. For example, when ambient growth conditions are provided, some seeds or spores germinate while others do not, and they are generally called non-dormant and dormant forms, respectively. The phenomenon of dormancy, or a period of quiescence, may be interpreted as an acquired character of plants when they moved to land from an aquatic habitat. The biological significance of dormancy in angiospermous seeds has been discussed very well by Bewley and Black (1982).

It is safe to assume that in an ideal situation the life cycle of a plant should keep on rolling uninterrupted. Ordinarily, most angiosperms temporarily terminate their life cycle by producing seeds. Those seeds, which do not immediately

continue into the next stage of germination, undergo a period of dormancy. In some specialized angiosperms, such as mangroves, the seeds (fruits), still attached to the parent plant, germinate precociously exhibiting the phenomenon of true vivipary (Goebel 1905; Juncosa 1982; Steeves and Sussex 1989). The nutrition of the embryo of such viviparous seedlings is facilitated from the side of the mother plant by the presence of water (Goebel 1905). In an investigation on a viviparous mangrove, Sussex (1975) hypothesizes with the available data that induction of dormancy is due to water stress in the seed. Dormancy can also be initiated by shrivelling or breaking the vascular connection in the funiculus, a mechanism which evidently prevents water and other nutrients from reaching the embryo in the seed (Guppy 1912; Ihle and Dure 1972). True vivipary can also be induced in the caryopses of wild oats (Hsiao and McIntyre 1988) and barley (Pope 1949) by providing high humidity to the target caryopses. These investigators suggest that during the maturation of the kernel, water supply to the embryo is somehow impeded, preventing the growth of the embryo in the caryopsis. Details such as these indicate two important points: (1) the life cycle basically represents a continuum: and (2) the dormancy is imposed on the seeds of plants inhabiting land. The absence of dormancy in an aquatic mangrove may be due to a lack of water stress in the seeds and, conversely, water stress can initiate dormancy. Differences of opinion are plentiful in the literature with respect to the actual physiological mechanisms controlling the onset of seed dormancy and its breakage. It is also worth approaching the problem of seed dormancy from a morphological and embryological perspective, and hypothesizing that the mechanism responsible for the appearance of dormancy in the seed must also be able to break dormancy, as explained by Sussex (1975).

The morphological and histological details on wild oats given in this book provide some insight into the problems of the onset of dormancy and of caryopsis germination. Soon after double fertilization, both the zygote and the primary endosperm nucleus divide rapidly. As the zygote divides immediately following syngamy, it is inappropriate to

envisage or speculate that the onset of dormancy is possible at the zygotic stage. Circumstantial structural evidence has been provided from ancient fossil seeds to suggest that the "post-zygotic quiescence may be a first step in the evolution of seed dormancy" (Mapes et al. 1989). Active cell divisions in the zygote result in the formation of an embryo. To keep pace with the rapid development of the embryo, the primary endosperm nucleus produces a large number of free nuclei. Free nuclear divisions continue asynchronously in the embryo sac until about 4 days after anthesis, when the cell walls begin to appear between the endosperm nuclei. The completion of cell wall formation, resulting in cellular endosperm, is achieved in about 7–8 days after anthesis. At about this stage, the proembryo will have been fully differentiated with all its parts, such as scutellum, root and shoot apices, etc. At the same time, the aleurone layer (outermost protein-rich layer of endosperm) around the embryo, and over the crease on the adaxial side of the caryopsis, becomes obvious, and it occurs long before the appearance of a similar layer on the abaxial side where the outermost layer of endosperm remains still "meristematic" at this stage.

By about 15–16 days after anthesis, the abaxial endosperm cells decline or stop dividing, and the outermost layer differentiates into the aleurone layer; by then the rest of the endosperm cells will have enlarged and accumulated abundant starch. The embryo also appears morphologically mature, and no more nuclear or cellular divisions are observed in any of the tissues in the caryopsis. These observations suggest that the early rapid growth and differentiation of the proembryo occurs as long as free-nuclear endosperm is still available within the embryo sac. The growth of the embryo slows down gradually as more endosperm cells are formed and starch grains begin to appear in them. The more centrally situated cells, and those toward the adaxial side, enlarge and enclose abundant starch, and also cause swelling of the caryopsis (Raju 1985). This distention caused by the starch-filled cells may also exert pressure on the ovule vasculature as suggested by Pope (1949) for barley, and by Hsiao and McIntyre (1988) for wild

oats impeding the supply of water and nutrients to the embryo through the ovular vasculature. The ovular strand becomes fully differentiated in wild oats after anthesis, especially after double fertilization in the embryo sac, in a manner similar to the wheat grain (Brenchley 1909, 1912; Frazier and Appalanaidu 1965) where the nutrients are carried into the endosperm through the ovular strand, chalaza, and nucellar tissue (hypostase). Such well developed vascular strands, which ordinarily transport water and nutrients, begin to be crushed or squeezed by the expanding endosperm tissue from within in about 20–22 days after anthesis (Figs. 186–189). Because of the obliteration of vascular strands the normal supply of water and other substances is cut off. Abundant break-down products accumulate in the region of obliterated vascular strands and give a brownish colouration. Such a strand is often called the "pigment strand."

Some histological changes involved during the development of the seed 15–16 days after anthesis seem to be critical in the onset of dormancy. The increase in starch content in the endosperm cells, the differentiation of a distinct aleurone layer, which covers both endosperm and embryo (Fig. 176), the modification of the chalazal nucellar-tissue with thick-walled cells to form the hypostase, and the squeezing or obliteration of the ovular vasculature caused by the swelling of the endosperm tissue may together bring about water stress in the caryopsis. These changes correspond to the report (McIntyre and Hsiao 1985) which shows the decline of embryo water content between 14–18 days from anthesis, corresponding to the structural differentiation of the aleurone layer (my study).

Water stress seems to be one of the earliest events to occur in the onset of dormancy in seeds (Sussex 1975; Walbot et al. 1975). The same causal factor may also operate in wild oats. The most important structural change that can be correlated with the beginning of obstruction of water supply is the differentiation of an aleurone layer, especially on the abaxial side, including the cheeks of the caryopsis. Although it is a part of the endosperm, the aleurone layer, with its protein-rich protoplast and thick cell walls, differs

from the rest of the endosperm in its behaviour (Raju 1985, 1986; Raju and Walther 1988). Despite the existence of a close correlation between the time of differentiation of the aleurone layer and the beginning of water stress (nonavailability of water to the embryo), still the latter process might start much earlier as reported for *Phaseolus vulgaris* (Walbot et al. 1975). The induction or onset of dormancy in the wild oat caryopsis is rather a gradual and prolonged process involving several structural changes, including the aleurone layer development in the seed, as described earlier.

Publications are innumerable in the field of physiology of seed dormancy and germination. Many physiological and biochemical mechanisms have been advanced to explain the breakage of dormancy or the process of germination in angiosperm seeds. Many mechanisms, feasible or speculative, have been described and discussed (Bewley and Black 1978, 1982; Blumenthal et al. 1986; Crocker 1906, 1916; Crocker and Barton 1953; Mayer 1980/81; Simpson 1978, 1990). The phenomenon of germination, which may be equivalent to primary root emergence, has been investigated in a wide variety of angiosperms. The wild oat has been a popular and important species in the physiological studies of dormancy and germination (Atwood 1914; Johnson 1935; Naylor 1983; Naylor and Jana 1976; Simpson 1978). There is very little information available, however, correlating caryopsis structure, dormancy and germination.

By definition, germination represents the emergence of the primary root (in most instances) from the seed or caryopsis (Bewley and Black 1978; Mayer 1980/81). Many physiological events precede the root growth in a seed and, unlike morphological root emergence, are invisible. Although many hormonal and nutritional factors are involved in germination, the primary causal factor(s) responsible for root emergence is still being debated (see Bewley and Black 1978; Mayer 1980/81; Simpson 1978, 1990). I have hypothesized in this book that increased water stress in the embryo brings about the onset of dormancy. If the same water stress is reduced by increasing the embryo water content, caryopsis germination occurs (Hsiao and McIntyre 1988; McIntyre and

Hsiao 1985). The dormant caryopses do not germinate unless they are mechanically injured. An injury increases water content in the embryo (Raju et al. 1988a), indicating that the embryo growth is essentially continuous and that dormancy is imposed on the embryo in intact caryopsis by exogenous factors. The embryo envelopes seem to regulate the movement of water to the embryo. In contrast to this, the water content in the embryo of viviparous forms is maintained at the optimum level so that seed germination or growth of embryo can occur unimpeded (Sussex 1975).

The embryo envelopes, which are still part of the caryopsis, may act as physical barriers and regulate the movement of water into and out of the caryopsis. Of all the envelopes, the aleurone layer along with the closely associated persistent nucellar epidermis, is important in caryopsis germination. If the aleurone layer is specifically injured by incising, pricking or scraping, the caryopses are stimulated to germinate (Raju and Tom 1986; Raju et al. 1988a). The aleurone cell walls are hygroscopic and become thick on hydration and thin on desiccation (Raju 1986; Raju and Walther 1988). The cell walls are known to contain phenolic compounds, glucans, hemicelluloses and other related compounds (Fulcher 1986; Jacobsen 1984). Their chemical composition is such that it can absorb water both from outside in the environment and inside from endosperm cells containing starch. The latter process keeps starch dry in the caryopsis. The cell walls can retain water depending on their chemical composition. In addition, the persistent nucellar membrane (epidermis) situated immediately external to the aleurone layer, and intimately associated with it, and the persisting hyaline layer of the inner integument together give a "cover glass" effect to the aleurone cells. This helps to prolong the retention of water in cell walls. The amount of water retained in the aleurone layer is probably adequate to protect the embryo and endosperm from serious desiccation. If, however, the envelopes, especially in the aleurone layer, are injured, the water content in the embryo is considerably increased to bring about caryopsis germination (McIntyre and Hsiao 1985; Raju et al. 1988a).

Thus, the caryopsis can be regarded as an example, which exhibits the phenomenon of integration among three components, the embryo, the endosperm and the embryo envelopes. All these integrate in an appropriate way to bring about caryopsis germination. The embryo envelopes in such an integrated and organized structure undergo structural specialization to impede normal water transport to the embryo, causing eventual dehydration within in the caryopsis. This process gradually establishes dormancy in the caryopsis. The envelopes can also, after a mechanical injury to them, permit adequate water supply to the embryo which over-rides the caryopsis dormancy, resulting in caryopsis germination.

There are many books, symposia volumes, etc., published on grasses, and most of them contain information on the physiological, taxonomic, cytological and economic importance of grasses (Barnard 1964; Gould 1968; Jones 1985; Soderstrom et al. 1986). A variety of phylogenetic trends have been recorded, but most of them are confined to grass taxa. There are a few publications which deal, rather casually, with relationships of grasses with other groups, both monocots and dicots. Even in discussions of this kind, reproductive data on grasses are minimal, while data on the morphology and embryology of monocots are almost absent (Dahlgren et al. 1985).

One interesting theory of phylogenetic antiquity of monocots has been proposed by Burger (1981), and this opposes the general belief that the monocots are recent and are derived from the dicots (see Cronquist 1968; Dahlgren et al. 1985). The grass taxa, including wild oats, are often considered as typical monocots, showing great uniformity in both vegetative and reproductive features, with few morphological variations. For example, the embryo development type described for *Avena fatua* is similar to those of other investigated taxa of grasses. The same is true of other embryological details. On the bases of certain vegetative characteristics with a few less important deviations, the grass taxa are morphologically quite homogeneous. If such an uniformity exists in vegetative features and presumably also in reproductive characters,

then one is confronted with an important question: Do these grasses represent an evolutionary culmination with a long ancestral history, or a recently evolved group with a great potential for future taxonomic and morphologic diversification. To answer this question sufficient comparative data are needed, not only from the monocot groups but from the putative monocot-like dicot taxa also (Burger 1977, 1981).

The grass embryo, with its associated characteristic parts, is unique. The probable homologies of these embryo parts, such as scutellum coleorhiza, etc., have been discussed for many years (Avery 1930; Arber 1934; Boyd 1932; Esau 1977). The scutellum, which is regarded as a single cotyledon, is present in all grass embryos and shows considerable morphological variation. While in most taxa it is a suctorial organ, in some it may become functionally a storage organ (Arber 1934; Eames 1961; Esau 1977). Nevertheless, a comparative study should be made to gain a better understanding of the evolutionary status of the scutellum in different taxa of the Gramineae and of other monocots. Often, the monocots and dicots are distinguished on the bases of the number of cotyledons and the topography of the shoot apical meristem. The wild oat embryo has been interpreted as having a terminal shoot apical meristem supported by two cotyledons, which eventually become functionally different. The scutellum forms the first cotyledon, functionally behaving as a suctorial organ, and the first leaf, which is the second cotyledon, as a photosynthetic organ. Such functional dimorphism of cotyledons has been reported in some monocots (Boyd 1932; Eames 1961). The occurrence of two cotyledons also has been recorded for some species of *Dioscorea*, a monocot genus (Lawton and Lawton 1967). One of its cotyledons is an absorbing organ and remains within the endosperm; the other emerges from the seed functioning as a photosynthetic leaf. It is also known that the pattern of early embryogenesis, up to the globular stage, is very similar both in monocots and dicots (Steeves and Sussex 1989). Evidence has appeared to support the view that in some monocots the shoot apical meristem is indeed terminal (Haccius 1952;

Natesh and Rau 1984; Swamy 1963; Swamy and Parameswaran 1962). My study of the wild oat embryo supports this view, and, in addition, that the shoot apical meristem is endogenous in origin like the root apical meristem, both meristems differentiating in a massive promeristem tissue. The occurrence of terminal shoot apical meristem in wild oats, a monocot, further bridges the phylogenetic gap between monocots and dicots.

The embryo of the wild oat, and possibly of other grasses, seems to carry certain morphological traits, some which could be considered phylogenetically primitive. The topography of the embryo with reference to endosperm (nutritive tissue) and the functional role of the embryo parts, such as scutellum, suspensor, etc., seems to indicate that the grass embryo does resemble in some respects the embryos of primitive vascular plants, as illustrated by Burger (1981). However, more comparative embryological and morphological studies need to be conducted on primitive vascular plants, and on both graminaceous and non-graminaceous monocots. The results of such studies could be significant in plant phylogenies.

EPILOGUE

The mandate of my investigation was to study in detail the development of the wild oat seed to obtain histological, embryological and developmental details that might be useful in future experimental work. This I have achieved. In addition, I have attempted to compare the data to the information available on seeds of other graminaceous and non-graminaceous taxa, and to explore the biological significance of the seed in the life cycle of an angiospermous plant. Some descriptive information, and a few morphological interpretations presented in these pages, may have phylogenetic implications, and they will be explored in future studies.

The angiospermous seed, which typifies a biological organization with its components, the embryo, the endosperm, and the embryo-envelopes, is a self-sustaining unit. Evolutionarily, the seed habit has a long history of 350 million years (Steeves 1983). During this period, it has passed through several successive ontogenetic changes, some of them adopted by different extant and extinct groups of vascular plants. One of these changes was "double fertilization," which probably occurred about 150 million years ago. It is a unique process, known only in angiosperms, and it has culminated in the angiospermous seed, possibly in the most perfect way. It is not surprising, therefore, to find that the angiosperms have successfully survived since the early Cretaceous, have profusely diversified, and have evolved unabatedly in the last 150 million years without changing or losing this unique mechanism and its associated product, the seed. Could there ever be a better mechanism to promote angiosperm survival, diversification, and evolution?

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FIGURES

1

FIGURE 1

Ideogram of a young panicle isolated from the flag-leaf sheath just three days before its emergence. The panicle is spread out to indicate branches in the erect position. The branches are usually pendant, as they do not have vascularized stems at this stage. The diagram shows nodes and internodes.

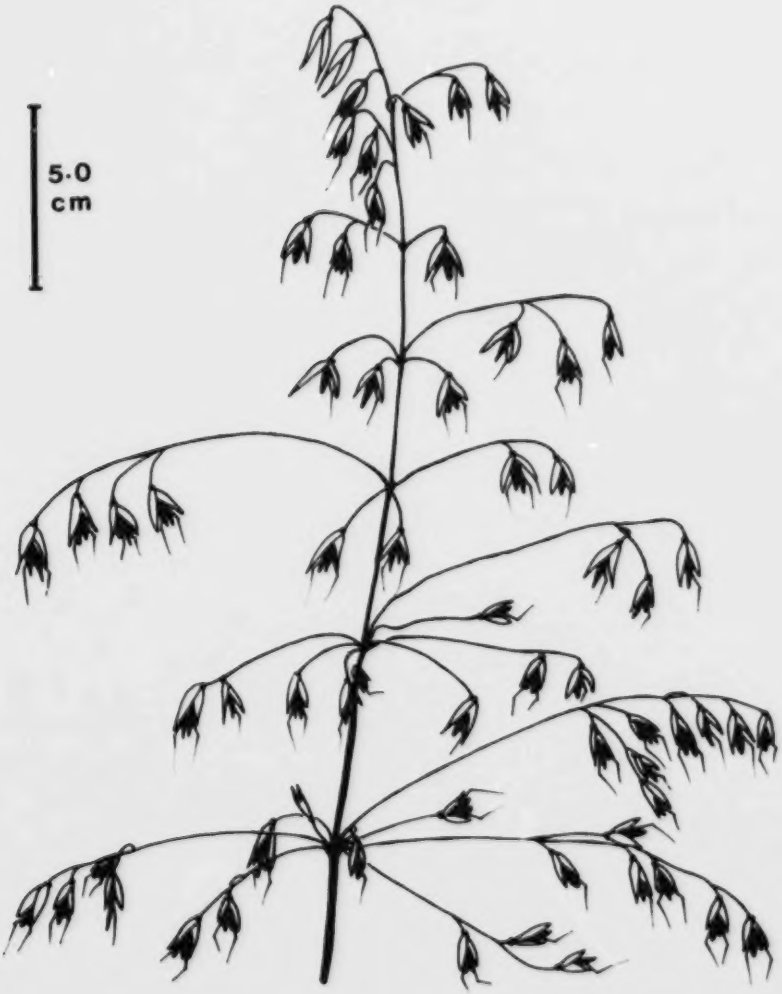

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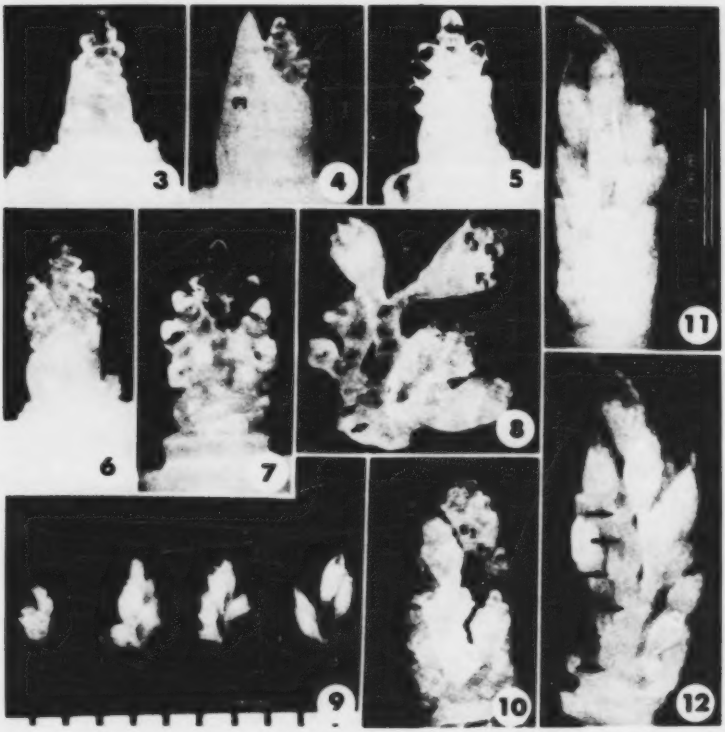
FIGURE 2

Ideogram of a small mature inflorescence showing main axis consisting of nodes and internodes, and branches at nodes. Glumes at the distal end are empty after the seeds have dropped. The mature floret-enclosed-caryopsis associated with the glumes are still present in the spikelets. In some only the secondary florets have dropped. Awns are dry and geniculate.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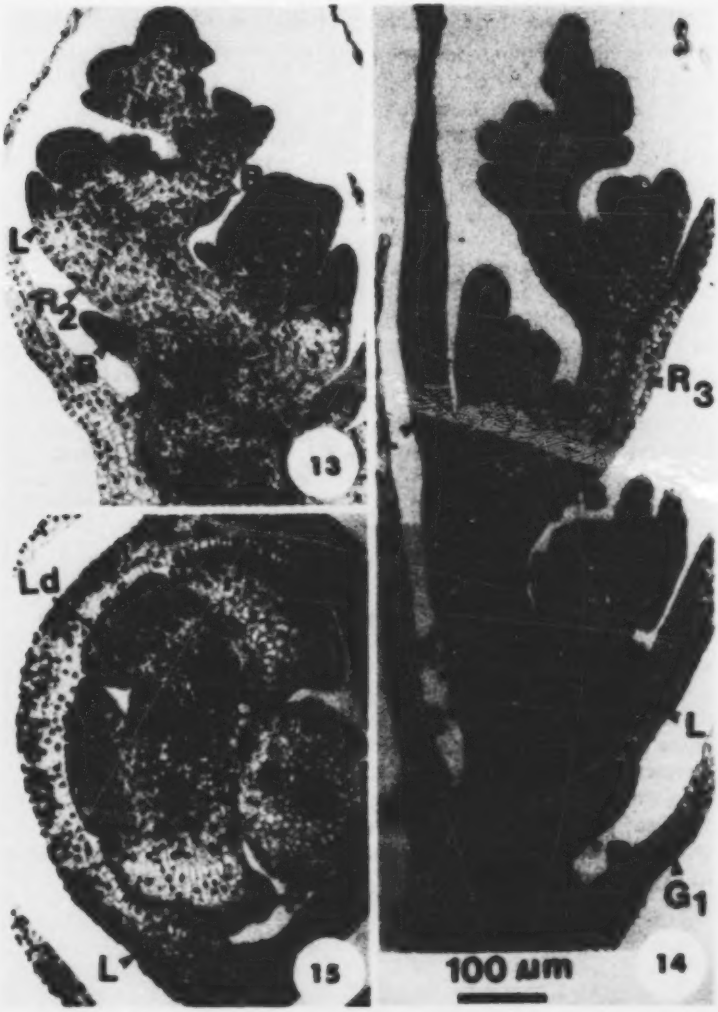
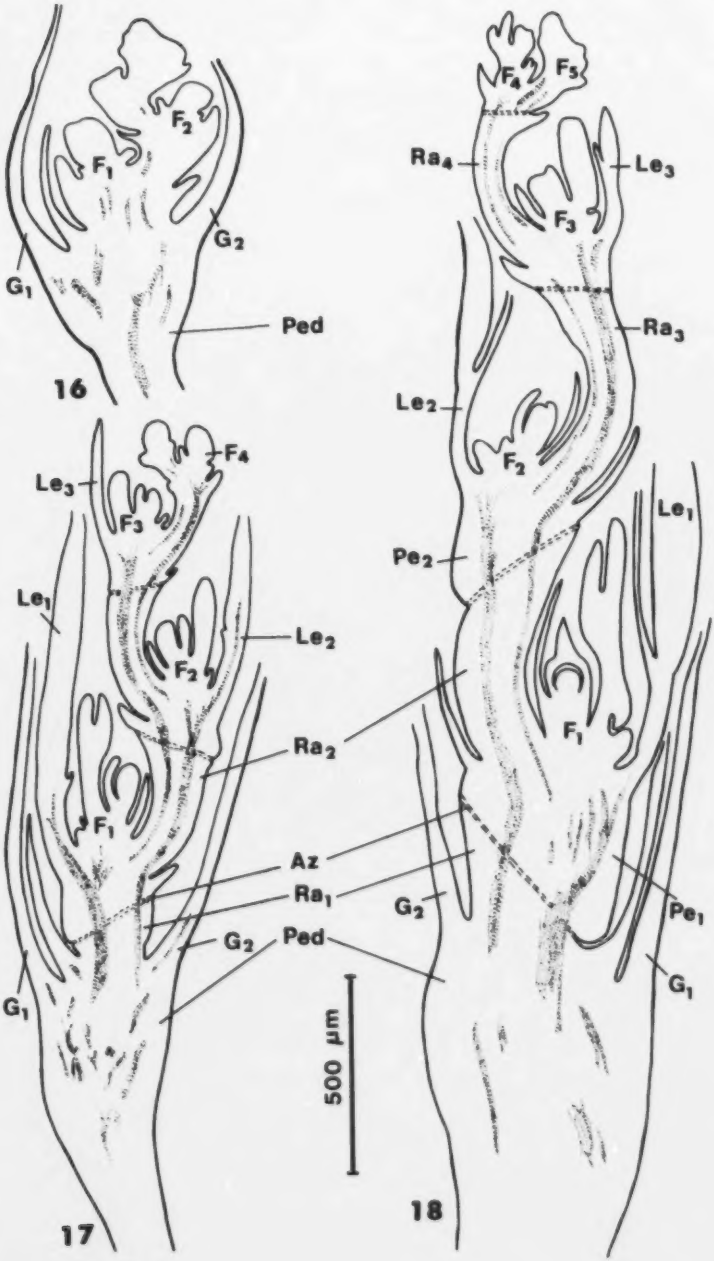
FIGURES 3-12

Inflorescence (panicle) development. Fig. 3, Floral apex transformed from a vegetative apex of a 16-day-old seedling. Fig. 4, Shoot tip, 20 days after germination, shows the partly differentiated distalmost spikelet of the inflorescence. The flag-leaf (7th leaf) still expanding. Fig. 5, Same with flag-leaf removed. First-formed or the oldest spikelet primordium of the inflorescence is seen. The subjacent primordia initiated later are less differentiated (younger). Fig. 6, A little later stage, 22 days after germination, to show differentiation of floret primordia in the spikelet initial. Fig. 7, Enlarged view of an inflorescence primordium with a terminal spikelet primordium in which glumes and some floret parts have differentiated. Fig. 8, Inflorescence (branch) primordium are the basal node, 25 days after germination, show older stages of development in the distal spikelet primordium. Younger stages of spikelets are seen proximally. Arrows point at young branch or spikelet primordia. Fig. 9, All branches from a young inflorescence have been removed and arranged in a sequence to show the difference in age and time of initiation. The distalmost (d) spikelets are better differentiated than those in the proximal part (a). Intermediate conditions prevail among those that lie in between (b, c). The pattern of maturity is basipetal. Fig. 10, Some young spikelet primordia are removed to show that the spikelets have a basipetal development, the distalmost one being the oldest. Arrow points at a young spikelet primordium. Fig. 11, Entire inflorescence, 35 days from germination, showing different stages of spikelet development, the distal most spikelet being the oldest. Fig. 12, Some spikelets in the same inflorescence are removed to expose the main axis with nodes (arrows) and internodes. Note that the glumes and lemma with its awn are better differentiated in most distally placed spikelet. (F_1, flag leaf primordium; $F_{1\text{-}3}$, florets of a spikelet; G_1, first or outer glume; G_2 second or inner glume; L, lemma). Magnification in all as in Fig. 11 except in Fig. 9.


L
R2
13
Ld
L
15
S
R3
L
G1
100 µm
14

FIGURES 13-15

Development and anatomy of the spikelet. Fig. 13, Sagittal section of a young spikelet with 5 floret primordia, of which only the basal two usually mature. The entire spikelet is covered by two glumes. Florets are here interpreted as terminal in origin. The rachilla is an axillary shoot, and subtending it is the bract (B) which eventually becomes insignificant or absorbed with the rest of the spikelet parts. Note the zig-zag nature of the rachillae and florets. Fig. 14, Longisection of an older spikelet showing the zig-zag or scorpioid or distichous arrangement of floret primordia and rachillae. The zig-zag nature of the axis is not as obvious as in Fig. 13. Fig. 15, Transection of a young floret to show the floral parts. The two provascular strands in the rachilla differentiate into inverted vascular bundles, placed opposite to each other, in a mature spikelet. (B, bract; F_1 and F_2, first and second floret primordia; G_1 and G_2, outer and inner glumes; L, lemma or lemma primordium; Ld, lodicule; P, palea; R, R_1, R_2, R_3, rachillae). All figures same magnification.


F2
F1
G2
G1
Ped
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F4
Le3
F3
Le1
Le2
F2
Ra2
F1
Az
Ra1
G2
Ped
G1
17
500 µm
F4
F3
Ra4
Le3
F3
Ra3
Le2
F2
Le1
Pe2
F1
G2
Pe1
G1
18

FIGURES 16-18

Spikelet morphology and anatomy. Fig. 16, Longisection drawings of a young spikelet with a scorpioid arrangement of florets. There are five floret primordia of which the lowermost two develop and produce viable seeds. The first and second glumes attached to the peduncle enclose the florets. Fig. 17, Longisection of an older spikelet showing the much straightened out spikelet axis and the florets appear to be laterally placed. Provascular strands are indicated. Each floret is subtended by a rachilla which is interpreted as a lateral shoot. The abscission zone arises at a very early stage between the pedicel and the rachilla. Fig. 18, An older spikelet with well differentiated floral parts. The first (primary) and second (secondary) florets usually develop normally. Abscission zones are indicated. (Az, abscission zone; F_1–F_5, floret primordia; G_1 and G_2, first and second glumes; Le_1–Le_3, lemma of florets; Pe_{1-2}, pedicel; Ped, peduncle; Ra_1–Ra_4, rachillae). All figures same magnification.

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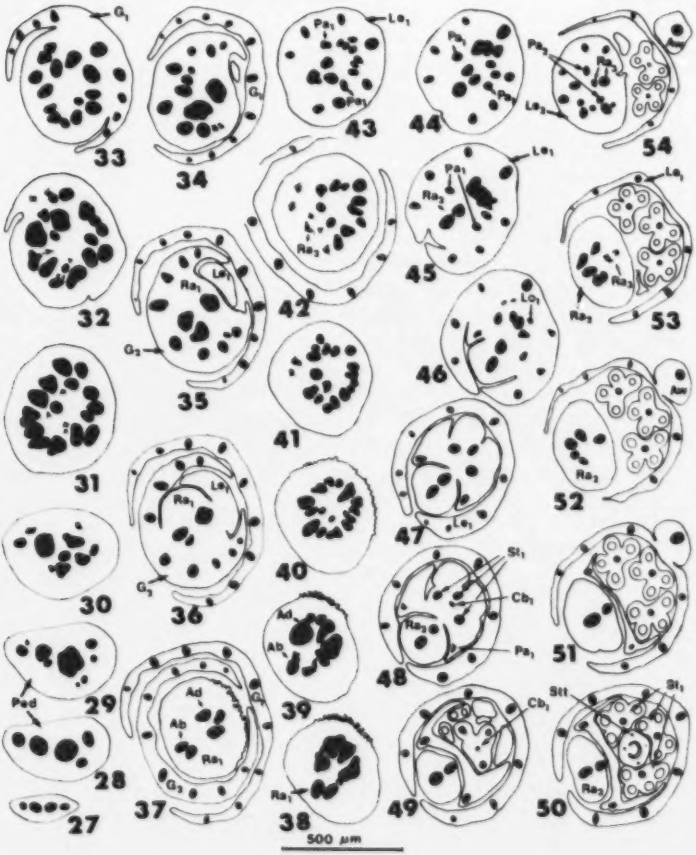
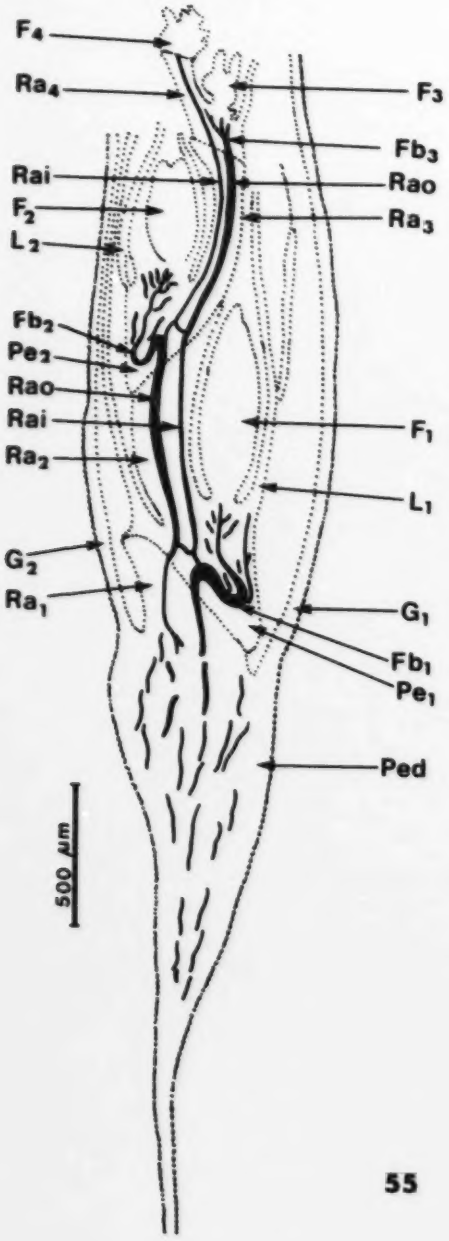
FIGURES 19-26

Floret anatomy. Fig. 19, Sagittal longisection of a spikelet with 6 floret primordia arranged in a zig-zag way. The distal 3 to 4 primordia do not develop into normal florets. Figs. 20-26, Selected transections at different levels of the base of a primary floret. (B, bract; C, commissural bundle of carpels and ovule; G_1 and G_2, outer and inner glumes; L, lemma; Ld, lodicule; P, palea or palea bundle; R, rachis or rachis bundles; S, stamen or stamen bundles). All figures same magnification.


500 µm

FIGURES 27-54

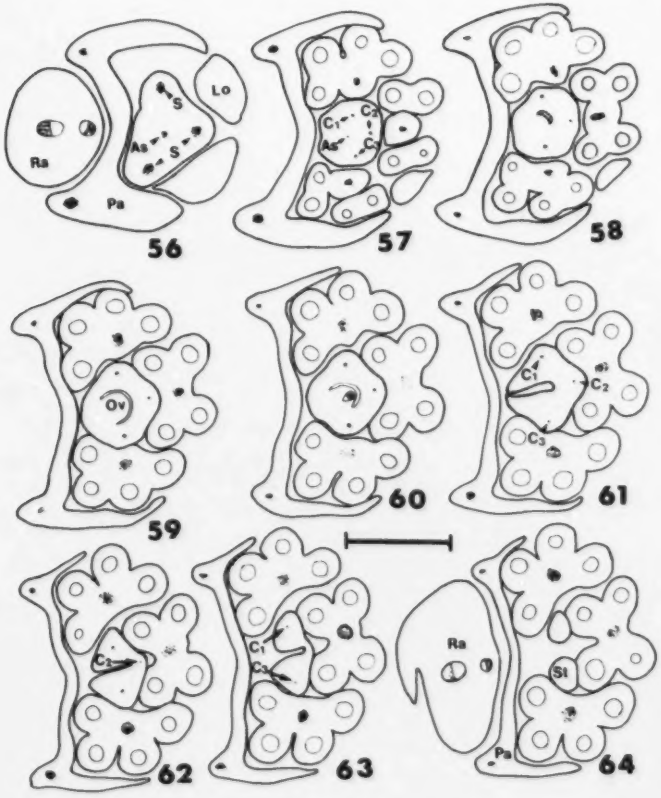
Anatomy of the spikelet (only selected transverse sections are drawn). Figs. 27-30, The peduncle of the spikelet is somewhat flat tending to become radial distally. The thin proximal end contains a row of 4 bundles which branch repeatedly to form many bundles. Figs. 31-33, Vascular bundles tend to show a ring-like arrangement. Fig. 34, After separation of first glume bundles, the rest of the bundles remain axial. Fig. 35, The second glume bundles become distinct, and many axial bundles are consolidated into a few larger bundles. Fig. 36, A few strands become distinct to produce the axial strands of the first rachilla. Figs. 37-41, After the second glume with its bundles has separated, the axial bundles divide to form a ring of bundles of the axis. Fig. 42, From these axial bundles, two bundles move out to form the second rachilla bundles. The separation or branching occurs before the lemma traces arise. Fig. 43, Immediately after the formation of second rachilla bundles, the axial bundles or floral bundles branch off to produce traces to lemma and palea in a distichous fashion. Fig. 44, Lemma and palea traces and second rachilla bundles become quite obvious. Fig. 45, The inner bundles of the second rachilla fuse to form a large common bundle. The two inverted bundles of the second rachilla appear distinct between the two palea bundles. Fig. 46, Higher up two lodicule traces differentiate each of which may branch again. Fig. 47, At a higher level beyond lodicule traces, three large bundles become evident, of the two laterals become the traces of two lateral stamens. Figs. 48-49, Of the three bundles seen in Fig. 47, the central bundle divides to give rise to the outer anterior stamen trace and the other inner remains as a commissural bundle (carpellary-ovule bundle). Fig. 50, Higher up the second rachilla with two inverted bundles is distinct. The commissural bundle divides to produce the carpellary and ovule bundles. Eventually the lateral tangential bundles become the traces for the two styles. Figs. 51-53, The outer bundle of the second rachilla branches to become the axial bundle of the second floret and part of the third rachilla. Fig. 54, After the bundles of the third rachilla are differentiated, the traces for second lemma are formed. (Ab, Abaxial first rachilla bundle; Ad, adaxial axial bundles; Aw, awn; Cb, commissural (carpellary) bundle of the first floret; G_1 and G_2, outer and inner glumes; Le_1 and Le_2, lemmas of the first and second florets; Lo_1, lodicule bundles of the first floret; Pa_1 and Pa_2, palea traces (bundles) of the first and second florets; Ped, peduncle of spikelet; Ra_1, first rachilla; R_2 and R_3, second and third rachilla traces (bundles); St_1, stamen traces (bundles) of first floret; Stt, stylar trace or bundle. All figures same magnification.


F4
Ra4
Rai
F2
L2
Fb2
Pe2
Rao
Rai
Ra2
G2
Ra1
F3
Fb3
Rao
Ra3
F1
L1
G1
Fb1
Pe1
Ped
500 µm

55

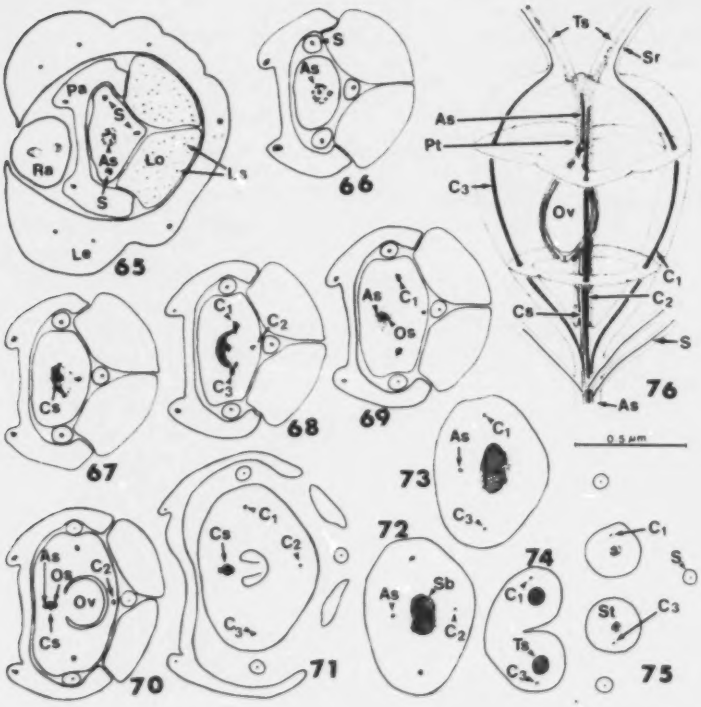
FIGURE 55

Sagittal section of a young spikelet showing four differentiated florets of which only the proximal two develop normally. It gives a semidiagrammatic view of the vasculature in the entire spikelet. (F_1–F_4, florets; Fb_1–Fb_3, floral bundles; G_1–G_2, outer and inner glumes; L_1–L_2, lemmas of first and second florets; Pe_1–Pe_2, pedicels of first and second florets; Ped, peduncle; Ra_1–Ra_4, rachillae of florets; Rai, inner bundle of rachilla; Rao, outer bundle of rachilla.)


Ra
Lo
S
As
S
Pa
56
C1
C2
As
C3
57
58
Ov
59
60
C1
C2
C3
61
C2
62
C1
C3
63
Ra
St
Pa
64

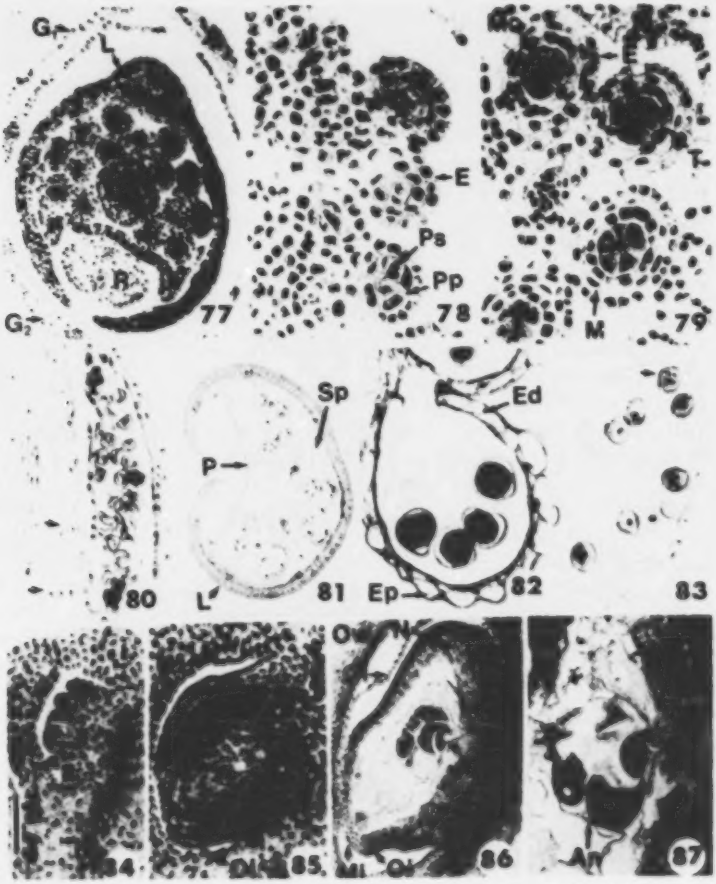
FIGURES 56-64

Cross sections of a young floret showing the anatomy of the pistil. Fig. 56, Section shows rachilla, lodicules, and palea. In the pistil, the stamen traces are present, and the central axial strand is distinct. Fig. 57, At a little higher level showing the remains of the axial (commissural) strand. The three carpellary bundles are clear. Figs. 58-60, At higher levels of pistil where the ovule has already differentiated, the vascular differentiation has not taken place. The axial strand has not reached the ovule yet. Figs. 61-62, In sections the ovule is distinct and the two lateral carpel bundles are distinct. Fig. 63, The middle second carpellary bundle has disappeared at this level, and the laterals contribute to two styles of the pistil. Fig. 64, No remains of the second carpellary bundle are found. The lateral carpels change distally into free styles. (As, axial strand; C_1–C_3, carpellary bundles; Pa, palea; Ra, rachilla; S, stamen bundle; St, stamen.) All figures same magnification. Bar is 200 μm.


Ps
S
Rs
As
Lo
Ls
S
Le
65
S
As
66
Ts
Sr
As
Pt
C3
Ov
C1
C2
Cs
S
As
76
0.5 µm
Cs
67
C1
C2
C3
68
As
C1
Os
69
As
C1
C3
73
C1
Cs
C2
C3
71
As
Os
C2
Ov
Cs
70
As
Sb
C2
72
C1
C1
Ts
C3
74
C1
S
St
C3
75

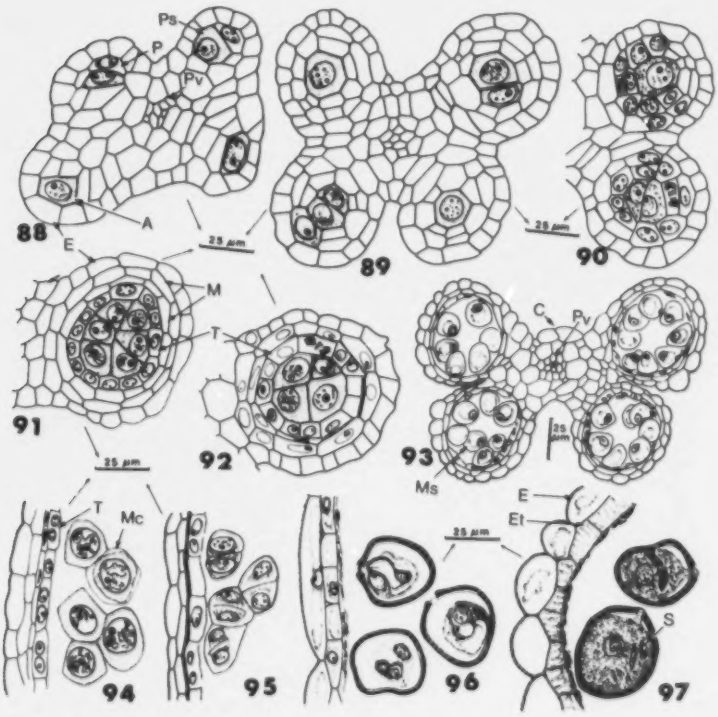
FIGURES 65-76

Anatomy of a floret showing changes in the vascular strands in the gynoecium. Fig. 65, Cross section of a floret with floral parts and their vascular strands. Note the large axial strand and the three differentiated stamen traces. Figs. 66-68, Show the differentiation of three carpellary traces from the axial strand. The commissural bundle composed of the axial and the ovular strands is clear. Fig. 69, Axial strand has branched to form the ovular strand, and continues as an axial strand higher up. Figs. 70-72, The commissural bundle continues as an axial strand after forming an ovular strand branch. Fig. 73, The abaxial carpellary bundle has disappeared and on the adaxial side the remains of the axial strand are observed. The transmitting tissues of the two styles can be seen. Figs. 74-75, Higher above the pistil continues to form two styles each having its own transmitting tissue. Fig. 76, Three dimensional diagram of a pistil to show the vascular anatomy and the approximate topography and position of the ovule and carpellary strands. (As, axial strands; C_1–C_3, carpellary bundles (traces); Cs, commissural strand; Le, lemma; Lo, lodicule strands; Ls, branched provascular lodicule strands; Os, ovule strand; Pa, palea; Pt, pigment strand; Ra, rachilla; S, stamen trace; Sb, stylar base; Sr, stylar bundle; St, style; Ts, transmitting tissue of style.) All figures except Fig. 76 which is diagrammatic.


G
R
77
E
Ps
Pp
78
M
79
80
Sp
P
L
81
Ed
Ep
82
83
84
Di
85
Mi
86
87

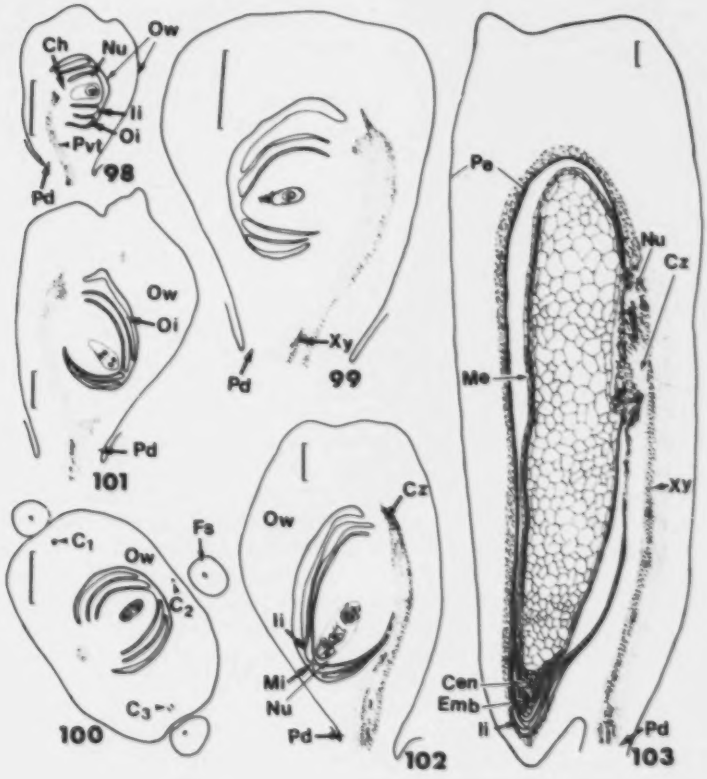
FIGURES 77-87

Microsporogenesis and male gametophyte development, and ovule and embryo sac development. Fig. 77, Transection of a young floret to show floral parts and rachilla. The central gynoecium is surrounded by three anthers, abaxial lemma, and adaxial palea. External to palea is the rachilla. The floret is covered by the glumes. Fig. 78, Section of parts of young anthers showing epidermis, primary parietal and sporogenous cells. Figure 79, At a later stage of anther development with microsporocytes surrounded by tapetum, two middle layers, and epidermis. Fig. 80, Longisection of anther with anther locule containing microspores and with a portion of connective showing characteristic reniform stomata (arrows). Fig. 81, Transection of floret at the level where stigmatic papillae and anthers are visible. Anther locules are about to dehisce releasing mature microspores. Fig. 82, Part of another locule with mature microspores. Mature wall is composed of epidermis and endothecium. Fig. 83, Each mature microspore contains two male cells and a tube nucleus (arrow). Fig. 84, Longisection of a young ovary with laterally placed young ovule with a megasporocyte in it. The integumental initials are well differentiated, and the ovule appears orthotropous at this stage. Fig. 85, A later stage of the ovary with an anatropous ovule, and a two-nucleate embryo sac. Note the position of the ovule. The ovular base is pushed distally because of the overgrowth of the adaxial side of the ovary. Fig. 86, Section of ovule at about the mature embryo sac stage showing the position of the chalaza in the nucellus and the antipodals. Because of over growth of the adaxial part of the ovary, both chalaza and the nucellus appear spread out. The embryo sac also elongates considerably and the antipodals appear to be situated lateral to the embryo sac. Fig. 87, Antipodal cells in the chalaza enlarged to show their haustorial behaviour. (Ah, antipodal haustorium; An, antipodals; Ch, chalaza; E, epidermis; Ed, endothecium; Ep, epidermis; G_1 and G_2, outer and inner glumes; L, lemma; M, middle layers; Mc, microsporocytes; Mi, micropyle; N, nucellus; Oi, outer integument; Ow, ovary wall; P, palea; Pp, primary parietal cell; Ps, primary sporogenous cell; R, rachilla; Sp, stigmatic papillae; T, tapetal layer.) All figures same magnification.


Ps
P
Pv
A
88
25 µm
89
90
E
M
T
91
92
C
Pv
93
Ms
25 µm
T
Mc
94
95
96
E
Et
S
97

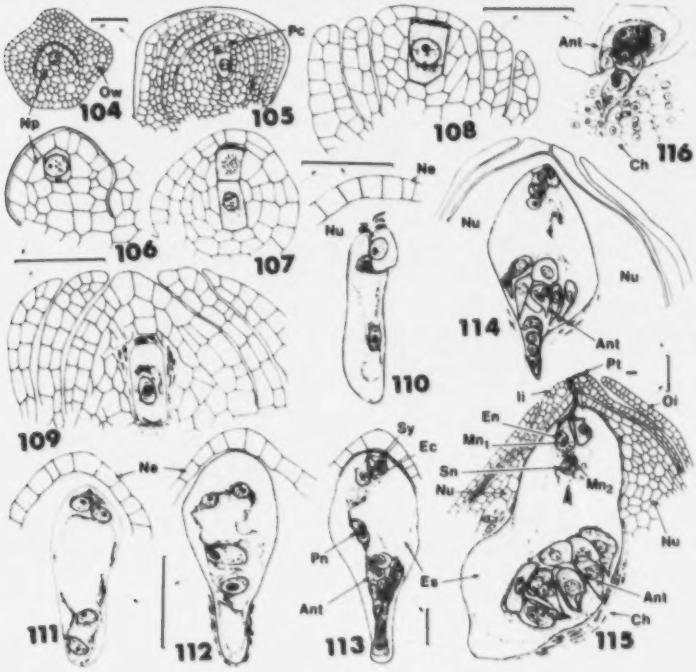
FIGURES 88-97

Microsporogenesis and male gametophyte development. Fig. 88, Transection of a young anther showing quadrilocular nature, and the initiation of archesporial cells. In a section a single subepidermal archesporial cell arises and differentiates by division to form parietal cell and primary sporogenous cell. Fig. 89, A quadrisporangiate anther with various stages of wall development and an increase in the number of sporogenous cells. Fig. 90, Anther sacs to show the sporogenous cell(s) surrounded by wall in which the outermost of the epidermis and the innermost is the tapetum. Fig. 91, More sporogenous cells in the middle surrounded by the wall composed of tapetum, two middle layers, and the epidermis. Fig. 92, Tapetal nuclei may divide to form two nuclei in each cell or with walls form more tapetal cells. Fig. 93, Part of the anther to show the wall of the anther and microsporocytes in the locule. The wall contains the epidermis, two middle layers, and the tapetal layer with binucleate or uninucleate cells. The inner middle layer has started degenerating. Fig. 94, A little later stage with degenerated inner middle layer, and the microsporocytes show first early-meiotic stage. Fig. 95, Longisection of anther locule with microsporocytes showing first meiotic division. One of the middle layers has begun to degenerate. Fig. 96, Longisection of anther locule showing monoporate microspores and the degenerated inner middle layer and the tapetum. Microspores are in the three-nucleate or binucleate stage. The outer wall of the epidermal cell has characteristic warty thickenings. Fig. 97, Part of mature anther locule with enlarged epidermal cells and the modified outer persistent middle layer of the wall showing characteristic banded thickenings, the endothecium. The mature monoporate microspores at the time of anther dehiscence is three nucleate—2 male cells and a tube nucleus. (A, archesporial cell; C, connective; E, epidermis; Et, endothecium; M, middle layers; Mc, microspore mother cells; Ms, microspores; Ps, primary sporogenous cell; Pv, provascular tissue; T, tapetum.) Small arrows emanating from figures pointing at the scale indicate respective magnifications.


Ch
Nu
Ow
Ii
Oi
Pvl
Pd
98
Ow
Oi
Pd
101
Pd
Xy
99
Pe
Nu
Cz
Me
Xy
Cen
Emb
Ii
Pd
103
C1
Ow
Fs
C2
C3
100
Cz
Ow
Ii
Mi
Nu
Pd
102

FIGURES 98-103

Ovule and seed development. Fig. 98, Sagittal section of a young ovary to show the lateral position of a young ovule in it. At the megasporocyte stage in the nucellus, the integuments have developed. The provascular tissue extending distally in the ovary wall is well developed, and appears to terminate at the base of the ovule. Fig. 99, Ovule at a later stage tending to become anatropous. The provascular tissue is extensive and most of it terminates at the base of the ovule; a part of it extends a little beyond and ends blindly. Some xylem is differentiated in the pedicel region. Fig. 100, Transection of ovary showing orthotropous condition of ovule. Massive nucellus and integuments are seen. Provascular strands of carpels are also observed. Provascular strands of the second carpel are very much reduced and often difficult to see. Ovary wall at this stage of ovule development is thick all around except on the abaxial side. Fig. 101, Longisection of ovary with a pendant ovule. At the proximal end of the outer integument on the abaxial side a characteristic "bump" is produced following the inner surface contour of the base of the style. Fig. 102, At mature embryo sac stage the embryo sac is surrounded by a massive nucellus which eventually is digested. More xylem tissue appears in the funiculus (attachment to carpel region). The ovule shows greater bending and the integuments on the adaxial side become crushed. The micropyle is organized by the inner integument. Fig. 103, In a caryopsis, about 6 days after anthesis, endosperm will have become cellular. The abaxial parts of endosperm are still meristematic. Note the extension of chalaza, ovule and also the stretching of carpel on the adaxial side. Note also full differentiation of xylem and there is no discontinuity in it. (C_1–C_3, carpellary bundles; Cen, cellular endosperm; Ch, chalaza; Cz, chalazal zone; Emb, embryo; Fs, filament of stamen; Ii, inner integument; Nu, nucellus; Oi, outer integument; Ow, ovary wall; Pd, pedicel; Pe, pericarp, Pvt, provascular tissue (strand); Xy, xylem.) Scale-bar magnification in each figure is 100 μm.


Ow
Np
104
Pc
105
106
107
108
Ant
Ch
116
Ne
Nu
110
Nu
Nu
114
Ant
Pt
Ii
Ol
En
Mn1
Sn
Nu
Mn2
Nu
109
Ne
111
112
Sy
Ec
Pn
Ant
Es
113
Ant
Ch
115

FIGURES 104-116

Megasporogenesis and embryo sac development. Fig. 104, Cross section of a young ovary with a young hypodermal archesporial cell in the ovular primordium. Fig. 105, Longisection of a young ovule with two integuments differentiated, each being two-layered. The archesporial cell has produced a primary parietal cell which has divided to form a few parietal cells. A large megasporocyte is visible. Fig. 106, a young nucellar primordium with a single archesporial cell. Fig. 107, A later stage showing the dyad with nuclear division in the upper dyad cell. Note that the nucellar epidermal cells may divide periclinally and anticlinally to produce a few more cells. Fig. 108, Higher magnification of a young ovule showing nucellus with degenerated parietal cells and the developing megasporocyte with a large nucleus. Fig. 109, A T-shaped megaspore tetrad in which the three micropylar megaspores have degenerated and the fourth has differentiated into an uni-nucleate embryo sac. Fig. 110, Nucellar primordium with two linear tetrads of megaspores; three in each have degenerated and fourth has developed into one- and two-nucleate embryo sacs. Fig. 111, Nucellus with a 4-nucleate embryo sac. Fig. 112, Nucellus with 4-nucleate embryo sac. Fig. 113, A fairly mature embryo sac showing the egg apparatus, two polars, and a large antipodal tissue derived from the original three antipodal cells. Fig. 114, A mature embryo sac with free antipodal cells just before fertilization. Fig. 115, A mature embryo sac at the stage of fertilization. The two polars together with the male nucleus fuse in triple fusion. The first male nucleus has fused with the egg in syngamy to produce the zygote. The embryo sac has already begun to expand. Fig. 116, Shows the haustorial nature of some antipodal cells within the embryo sac. (Ant, antipodal cells; Ch, chalaza; En, egg nucleus; Es, embryo sac; Ii, inner integument; Mn_1 and Mn_2, male nuclei; Ne, nucellar epidermis; Ow, ovary wall; Pc, parietal cells; Pn, polar nucleus; Sn, secondary nucleus.) Thin arrow from figures points at the magnification scale; scale in all is 50 μm.

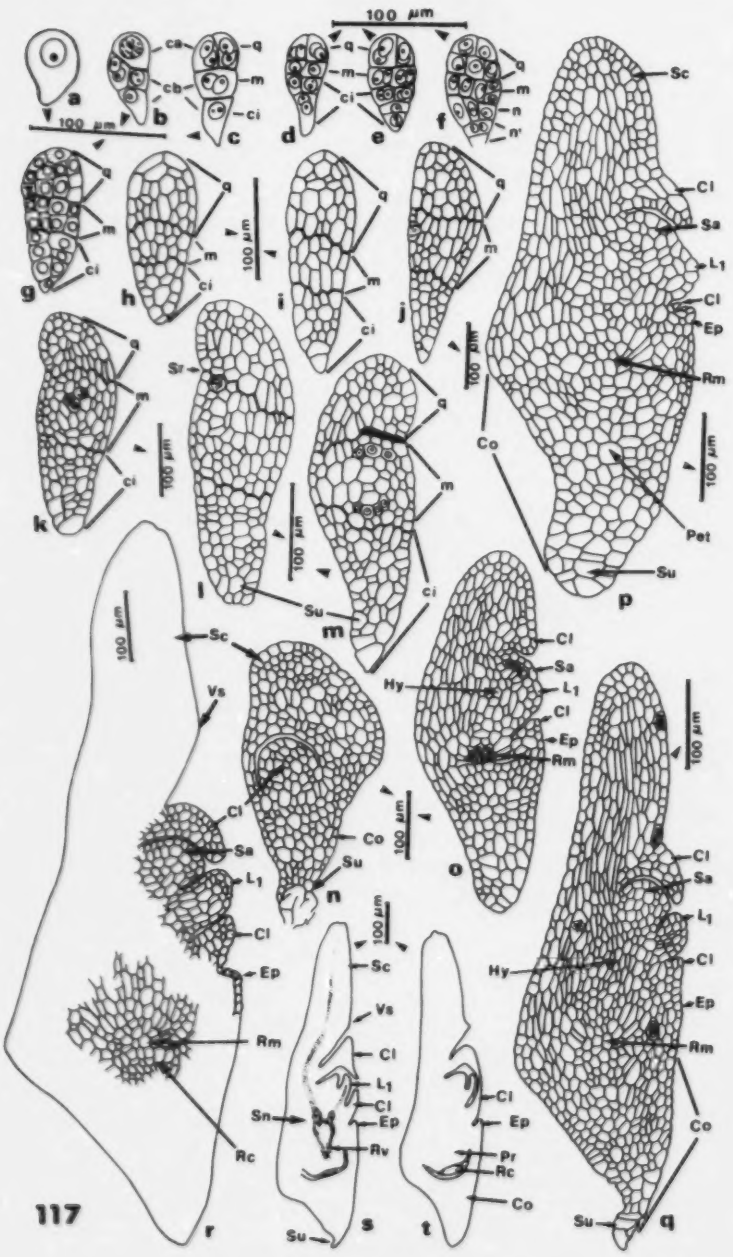
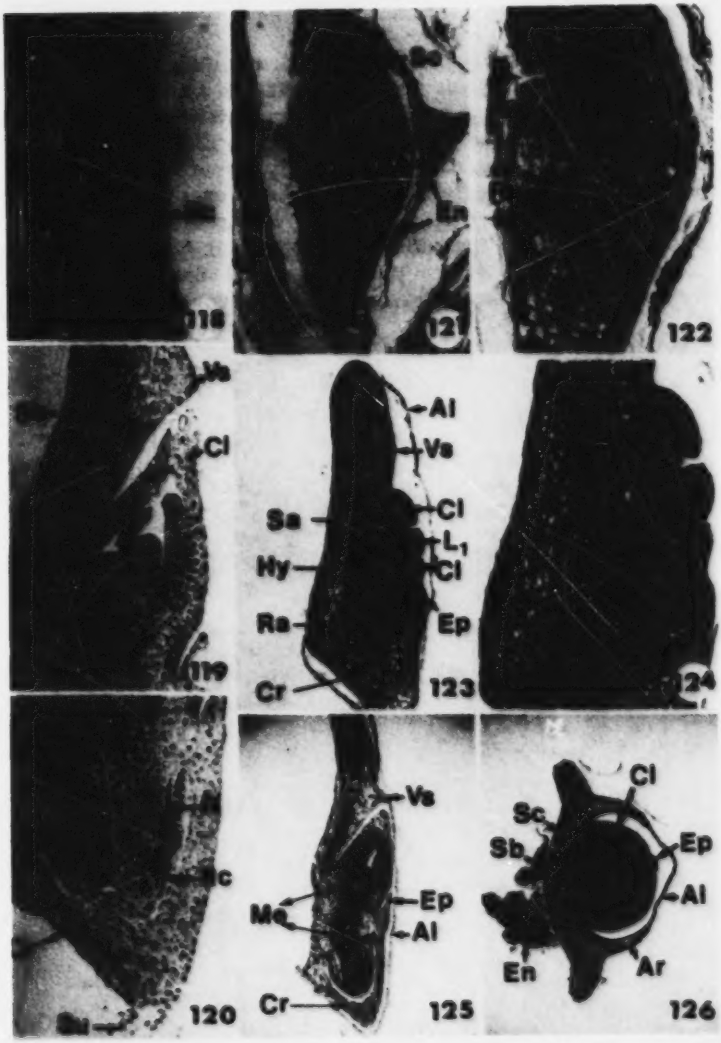

100 µm
a
b
ca
cb
c
q
m
ci
d
e
f
n
n'
g
h
i
j
k
Str
l
Su
m
Sc
Cl
Sa
L1
Ep
Rm
Co
Pet
p
Vs
Hy
n
o
Sn
Rv
Pr
Rc
r
s
t
q
117

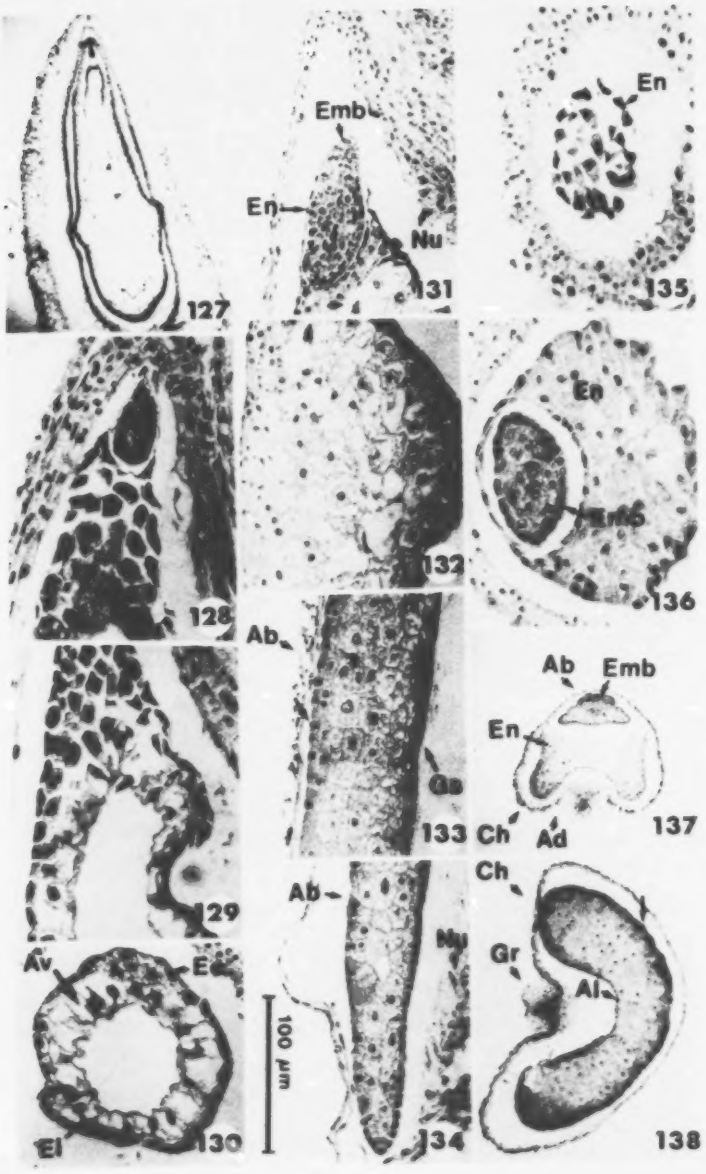
FIGURE 117

Embryogenesis. a, zygote; b-t, various stages of embryo development. Embryogenic terms: ca, terminal cell; cb, basal cell; ci, lower daughter cell of basal cell; m, upper daughter cell of basal cell; n, n', derivatives of ci; q, quadrant. (Embryo parts: Cl, coleoptile; Co, coleorhiza; Ep, epiblast; Hy, hypocotyl; L_1, first leaf (second cotyledon); Pet, proembryonic tissue; Pr, primary root; Rc, root cap; Rm, root meristem; Rv, root provasculature; Sa, shoot apical meristem; Sc, scutellum (first cotyledon); Sr, scutellar rim; Su, suspensor, Vs, ventral (adaxial) scale.) Scales pointed by arrowheads are the magnifications of the respective figures.


118
121
122
Ve
Cl
119
Al
Ve
Cl
Sa
Hy
Cl
Ra
Ep
Cr
123
124
Ve
Ep
Mc
Al
Cr
125
Cl
Sc
Sb
Ep
Al
En
Ar
126
120

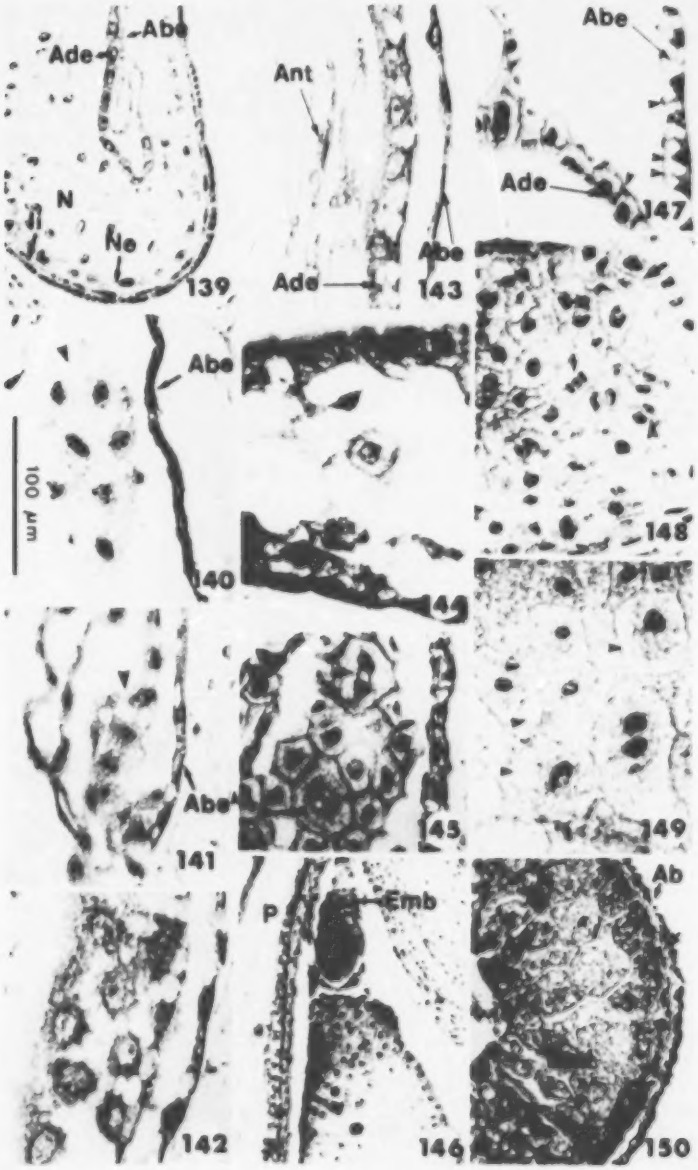
FIGURES 118-126

Early embryo development. Figs. 118-120, Sagittal sections of distal, middle and proximal parts of the same embryo isolated from a caryopsis, 20 days after anthesis. Provasculature is well developed. All parts of a mature embryo are differentiated at this stage. Fig. 121, Sagittal section of a young embryo, 5 days after anthesis. Fig. 122, Enlarged view of the same to show the differentiation of shoot and root apical meristems. Note also the region (large arrow head) where the adaxial part of the scutellum separates from the proximal part of the embryo (proembryo). Fig. 123, Sagittal section of the embryo from a caryopsis, 8 days after anthesis. Most parts of a normal mature embryo are differentiated. Shoot and root apical meristems are also obvious. Fig. 124, Enlarged view of a part of the embryo to show the meristems, coleoptile, first leaf primordium, and the epiblast region. Fig. 125, Section of an embryo isolated from a mature caryopsis, dislodged from the parent plant, with all embryo parts differentiated. Note the region (mesocotyl) between the scutellar and coleoptilar nodes. Fig. 126, Cross section at the coleoptile node to show the scutellar and coleoptilar bundles. (Al, aleurone layer; Ar, adaxial ridge; Cl, coleoptile; Cr, coleorhiza; En, endosperm; Ep, epiblast (region); Hy, hypocotyl; L_1, first leaf (second cotyledon); Me, mesocotyl; Pvt, provascular tissue; R, primary root; Ra, root apical meristem; Rc, root cap; Sa, shoot apical meristem; Sb, scutellar bundle; Sc, scutellum (first cotyledon); Su, suspensor; Vs, ventral scale (adaxial scale).) All figures same magnification.


127
Emb
En
Nu
131
En
135
128
132
En
Emb
136
Ab
Gb
133
Ab
Emb
En
Ch
Ad
137
129
Av
El
130
Ab
Nu
100 µm
134
Ch
Gr
Al
138

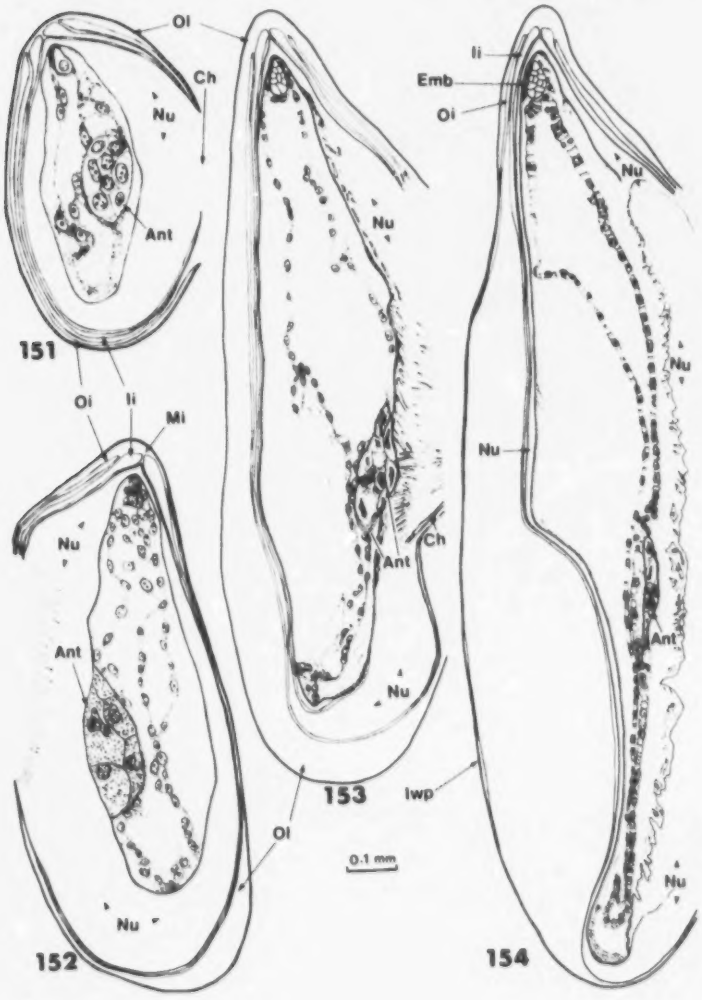
FIGURES 127-138

Development of endosperm. Fig. 127, Longisection of a young caryopsis showing free-nuclear endosperm in the embryo sac (arrow heads). The proembryo is at the micropylar end. Fig. 128, Micropylar end of a young seed with the proembryo surrounded by endosperm cells some of which do not possess cell walls. In others the nuclei divide and walls between them are formed (arrow head). Fig. 129, The free endosperm nuclei placed in the periphery have been separated by cell walls. Such cells have now divided periclinally to form a two-layered endosperm. The inner alveolar cells are larger than cells in the outer layer, and do not usually divide or contribute to endosperm. The outer cells, especially on the abaxial side, divide periclinally to produce more endosperm cells toward inside. Many alveolar cells obliterate, but in others the inner periclinal walls appear sealing the alveolar cells. Fig. 130, Cross section of two-layered endosperm, the inner alveolar cells are quite clear. The outer layer divides again to form a few more layers. Figs. 131-134, Longisections of endosperms at different levels in a young seed (5 days after anthesis) to show the morphology of endosperm. Cell wall formation in endosperm is completed. Fig. 131, Micropylar end of the seed showing a young embryo surrounded by endosperm. Most of the nucellus has been digested. Some endosperm cells, a little distal to embryo, are large and vacuolate. The cell walls in them are not distinct and the nuclei begin to degenerate (arrow). Fig. 132, A part of of endosperm distal to embryo showing larger centrally situated endosperm cells surrounded by smaller radially compressed cells. The cells in the abaxial outermost layer become meristematic. Fig. 133, The outermost layer of endosperm on groove or adaxial side has ceased to divide to form the aleurone layer, and on the abaxial side a similar layer remains meristematic (arrow). Fig. 134, Endosperm in the proximal part of embryo sac is cellularized. Obliterated nucellar tissue is seen on the adaxial side. Fig. 135, Cross section of endosperm near the embryo to show irregular cells, and cell walls between them are not clear; such cells are seen around and just distal to the embryo. Most peripherally placed cells become the aleurone cells covering the adaxial side of the embryo. Fig. 136, Cross section of caryopsis, 10 days after anthesis, to show the young embryo surrounded by the endosperm. Very little endosperm (2 layers) is present on the adaxial side of the embryo. Eventually, the inner layer is digested and outer differentiates into the aleurone layer. Fig. 137, Cross section of caryopsis (11 days after anthesis) showing the central and cheek parts of endosperm. Fig. 138, Cross section of mid-region of a young caryopsis (11 days after anthesis) with groove and cheek regions. On the adaxial side of endosperm aleurone layer is differentiated, but on the abaxial side, including the cheek regions, the outermost layer is still meristematic (arrow). (Ab, abaxial side; Ad, adaxial side; Av, alveolar cells; Ch, chalaza; Ei, inner endosperm layer; Emb, embryo; En, endosperm; Eo, outer endosperm layer; Gr, groove; Gs, groove side (adaxial); Nu, nucellus.) All figures same magnification.


Abe
Ade
N
Ne
139
Ant
Ade
Abe
143
Abe
Ade
147
Abe
100 µm
140
148
141
Abe
145
149
142
P
Emb
146
Ab
150

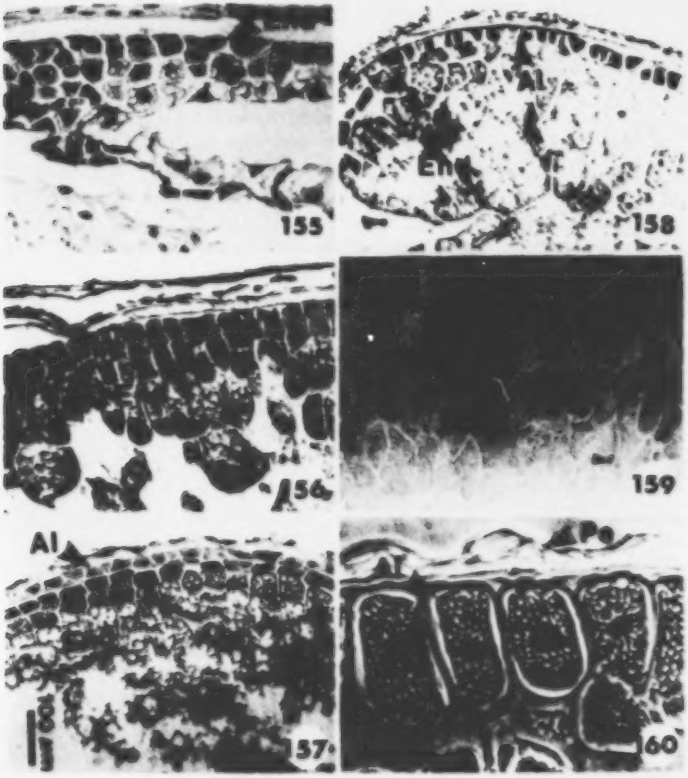
FIGURES 139-150

Morphology and development of endosperm cells. Fig. 139, Longisection of a young seed, 4 days after anthesis, showing free-nuclear endosperm which is in close contact with nucellus. Fig. 140, Surface view of free-nuclear endosperm. Note the formation of vacuoles between nuclei (arrow head). Endosperm nuclei in the abaxial region lie in a row separated by vacuoles. Fig. 141, Vacuoles between nuclei are common (arrow head). Fig. 142, Surface view of endosperm to show the appearance of vacuoles before cell wall formation between nuclei. Fig. 143, Longisection of a young seed, 4 days after anthesis, to show the degenerating antipodals. Note the vacuoles between endosperm nuclei. Fig. 144, Surface view with an endosperm nucleus surrounded by a cell wall without going through mitosis. Fig. 145, Endosperm tissue with nuclei and cell walls. Cell walls are formed without mitosis. Appearance of vacuoles between nuclei during nuclear separation (arrows). Fig. 146, Longisection of a young seed, 5 days after anthesis, with endosperm tissue at the micropylar end distal to the embryo. Note the large alveolar cells toward the centre of the endosperm. The younger cells formed in the periphery push the older alveolar cells toward the centre. Some endosperm cells toward the middle are open-ended without inner periclinal walls. Growth of endosperm is centrifugal with more recently formed cells present toward the periphery. Open-ended cells are common more on the abaxial side of the endosperm than on the adaxial side. Fig. 147, A part of endosperm with nuclei distributed adaxially and abaxially. Walls between nuclei are distinct (arrow heads). Fig. 148, Endosperm tissue about 6 days after anthesis, with a few dividing nuclei. Some nuclei divide and walls are not formed (small arrow), and a few others show cell wall formation (large arrow head). In a few others the already formed cells with their own walls are closely apposed and cell walls appear distinct (large arrow). Fig. 149, Endosperm tissue, 7 days after anthesis, shows distinct cell walls. Most cells are uninucleate, and nuclei often show signs of degeneration. The cells contain large numbers of vesicles in which starch grains begin to appear (arrows). Fig. 150, Endosperm in a caryopsis, 10 days after anthesis, with adaxially differentiated aleurone layer. Abaxially the outermost endosperm layer is still meristematic (arrow) and aleurone layer is not differentiated yet. Starch synthesis is extensive in more centrally situated endosperm cells, and occurs earlier than in the more peripherally placed cells. (Abe, abaxial endosperm; Ade, adaxial endosperm; Al, aleurone layer; Ant, antipodals; End, endosperm; Ii, inner integument; N, nucellus; Ne, nucellar epidermis; P, pericarp tissue.) All figures same magnification.


Ol
Ch
Nu
Ant
151
Oi
Ii
Mi
Nu
Ant
Nu
152
Ol
Nu
Ant
Ch
Nu
153
Ii
Emb
Oi
Nu
Nu
Nu
Ant
Nu
lwp
154
0.1 mm

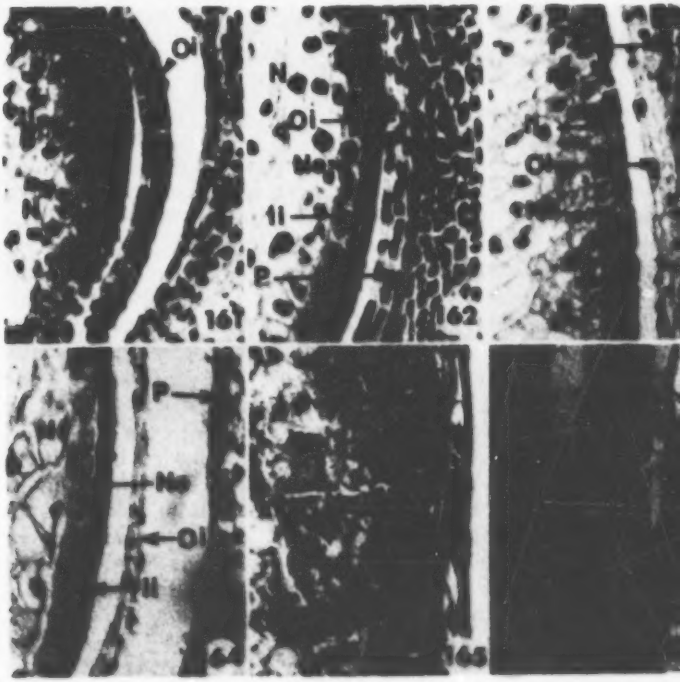
FIGURES 151-154

Endosperm development and changes in ovule morphology. Fig. 151, Sagittal view of the ovule, one day after anthesis, showing a zygote, many endosperm nuclei, and antipodal tissue in the embryo sac. The ovule begins to elongate and the embryo sac tends to follow the ovule elongation. The antipodals appear to be placed in a lateral position because of overgrowth or elongation of embryo sac on its abaxial side. Fig. 152, Embryo sac, three days after anthesis, with a proembryo and many endosperm nuclei. The antipodals show signs of degeneration. The ovule has elongated considerably. Fig. 153, The ovule, four days after anthesis, with degenerating antipodals and with many endosperm nuclei placed peripherally in the embryo sac. A proembryo at micropylar end is present. Fig. 154, The ovule, also 4 days after anthesis, contains a large number of endosperm nuclei which are placed peripherally, and this condition is not always uniformly found in the embryo sac because of distortions presumably caused during processing of materials. Vacuoles first appear between nuclei and then the radial cell walls appear to organize the alveolar cells. Eventually the endosperm undergoes centrifugal growth. Cell walls appear earlier in the micropylar end than other regions of the embryo sac. The original chalazal region below the antipodals and the nucellus stretch longitudinally to organize the pigment strand in the mature caryopsis. The endosperm nuclei on the adaxial side (groove side) arrange themselves in such a way that they appear to be organized, and it occurs much earlier than in other parts of the young seed. (Ant, antipodals; Ch, chalaza; Emb, embryo; Ii, inner integument; Iwp, inner wall of pericarp; Mi, micropyle; Nu, nucellus; Oi, outer integument; Ol, ovary locule.) All figures same magnification.


155
Al
En
158
156
159
Al
157
Po
160

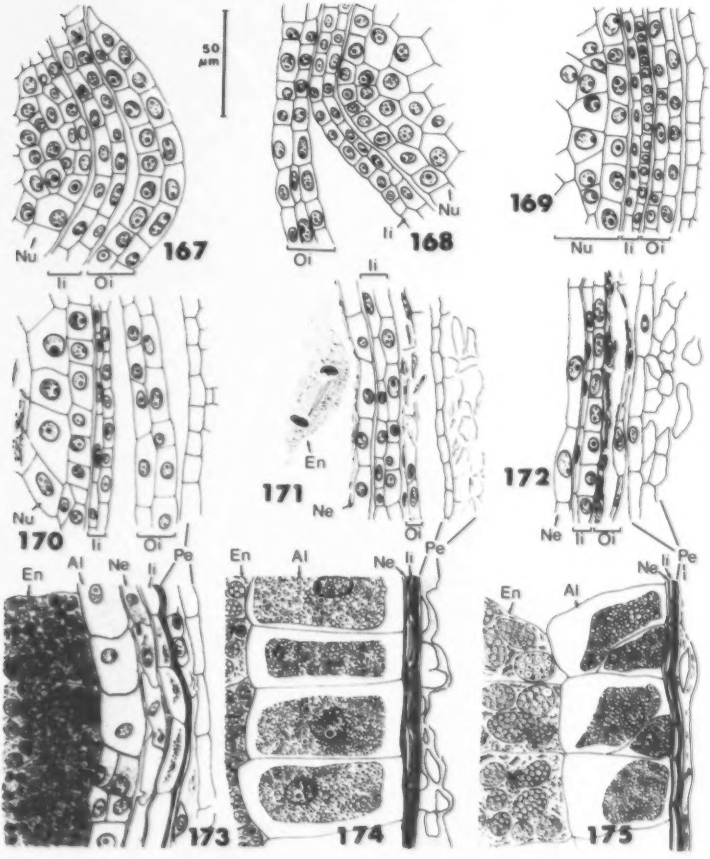
FIGURES 155-160

Endosperm and aleurone layer development. Fig. 155, Endosperm, four days after anthesis. Cell wall formation in free endosperm nuclei has already begun. No starch in cells is observed. Fig. 156, Endosperm nine days after anthesis, with no aleurone layer differentiated on the abaxial side yet; meristematic layers in the outermost region of endosperm are present. Note abundant starch in inner endosperm cells. Fig. 157, Endosperm, fifteen days after anthesis, with the outermost layer on the abaxial side differentiating to form the aleurone layer. Large inner cells of endosperm contain starch. Fig. 158, Endosperm, 20 days after anthesis, with outermost abaxial layer differentiated into the aleurone layer. Large inner cells contain starch. Fig. 159, Endosperm, in a mature caryopsis with well-differentiated aleurone layer in a section stained by using Feulgen technique. Nuclei in the aleurone layer appear normal. In the endosperm cells the nuclei show different degrees of degeneration or morphological breakdown. Small arrows point at degenerating nuclei (DNA). Starch is abundant in the inner cells. Fig. 160, Section of a mature caryposis to show endosperm, aleurone layer, and pericarp tissue. Note the vesiculate nature of the cytoplasm in the aleurone cells, and also the thick walls of aleurone cells. (Al, aleurone cell; End, endosperm; Pe, pericarp; S, starch.) All figures same magnification.


Ol
N
Ol
M
11
P
161
162
P
Ne
Ol
11
165

FIGURES 161-166

Development of embryo envelopes. Fig. 161, Longisection of ovary showing ovary wall (pericarp), integuments and nucellus of the ovule. Integuments, the inner and outer, are two-layered each. Fig. 162, After fertilization many changes occur in the nucellus, integuments and pericarp. The two laryers of the outer integument begin to degenerate. Fig. 163, During development both inner and outer integuments become radially compressed, and the outer integument becomes crushed or obliterated. Fig. 164, Note degeneration or obliteration of outer integument. Pericarp tissue gets also radially compressed. Fig. 165, In a caryopsis, 20 days after anthesis, endosperm tissue is well developed and the cells are enlarged enclosing abundant starch. The outermost persistent aleurone layer can be recognized. The outer integument is completely resorbed. Fig. 166, Embryo envelopes are well developed in a mature caryopsis. Nucellar epidermis, inner integument and the innermost layer of pericarp persist as cuticular layers. The aleurone envelope with its characteristic cell walls and protoplast remains distinct. (Al, aleurone layer; En, endosperm; Ii, inner integument; N, nucellus; Ne, nucellar epidermis; Oi, outer integument; P, pericarp.) All figures same magnification.


50 µm
Nu
Ii
Oi
167
Nu
Ii
168
169
Nu
Ii
Oi
170
Nu
Ii
Oi
171
Ii
En
Ne
Oi
172
Ne
Ii
Oi
Pe
En
Al
Ne
Ii
Pe
173
En
Al
Ne
Ii
Pe
174
Ne
Ii
Pe
En
Al
175

FIGURES 167-175

Development of seed coat and other envelopes. Fig. 167, A part of a young ovule to show the two 2-layered integuments, the inner and outer. Figs. 168-169, Later stages of the above showing the bilayered inner and outer integuments covering the nucellus. Fig. 170, At about the mature embryo sac stage considerable amount of nucellus is digested and nucellar epidermis appears differentiated. Fig. 171, After fertilization many changes occur. Endosperm nuclei begin to divide, and most of the nucellus except the nucellar epidermis becomes digested. Considerable elongation of cells occurs in the nucellar epidermis, the inner integument and in the innermost layer of the pericarp. Cells of the outer integument begin to disintegrate. Fig. 172, The outer integument is almost resorbed. The inner layer of the inner integument shows signs of cellular breakdown and eventually resorbed. Fig. 173, In a fairly mature caryopsis the outermost layer of endosperm becomes differentiated into the aleurone layer. The nucellar epidermis begins to degenerate. The inner layer of inner integument gets crushed. The pericarp tissue also shows considerable distortion. Fig. 174, The aleurone cells become radially elongated, and in the processed slides their walls appear thin. The nucellar epidermis is crushed leaving behind a cutinaceous layer closely associated with the persistent aleurone layer. Similarly, the outer layer of cells of inner integument is also obliterated and persists as a cutinaceous layer. Fig. 175, "Wall" of a mature caryopsis consists of a massive endosperm tissue with a layer of differentiated aleurone layer. Aleurone cells contain vesiculate cytoplasm, often filled with contents and nuclei, which may or may not appear normal. The nucellar epidermis persists as a thin membrane and also the inner integument. However, the latter appears as a thicker persistent membrane. External to this membrane is a thin layer often associated with degenerated cells of pericarp. The innermost wall of the pericarp persists as a thin membrane. (Al, aleurone layer of cells; En, endosperm; Ii, inner integument; Ne, nucellar epidermis; Nu, nucellus; Oi, outer integument; Pe, pericarp tissue.) All figures same magnification.

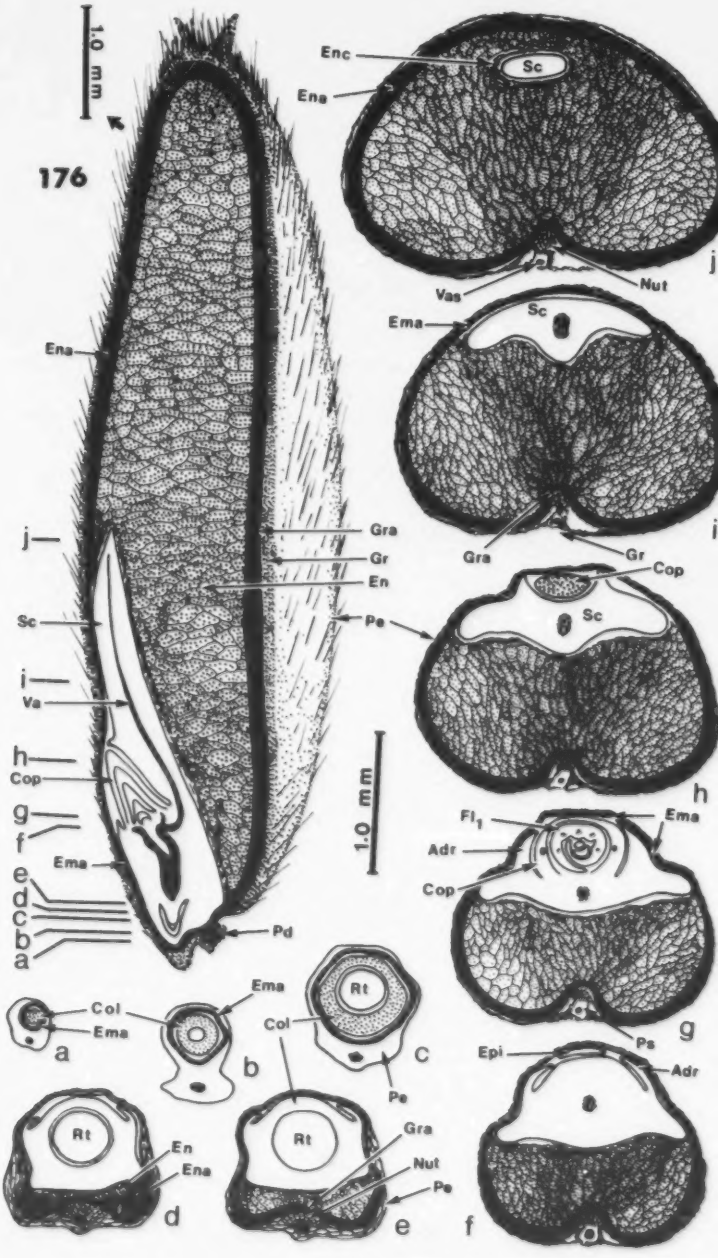
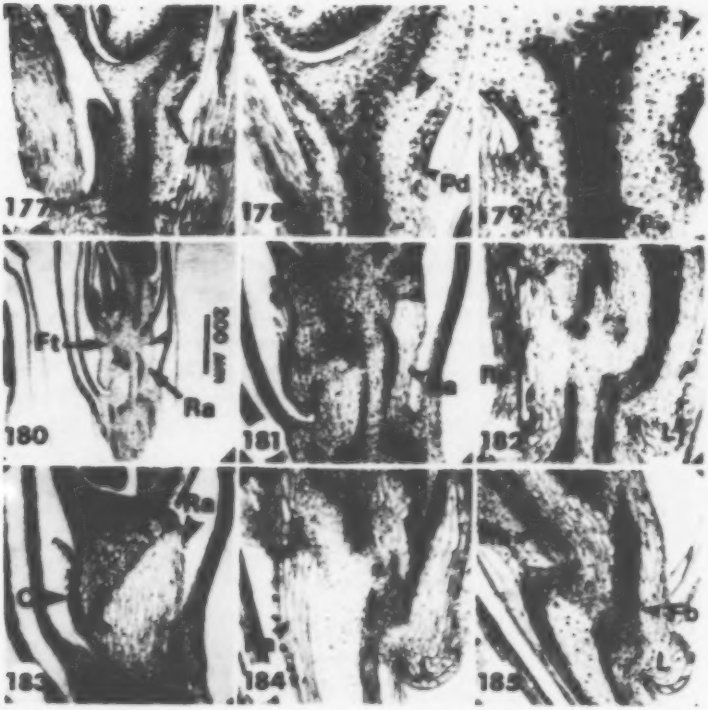

1.0 mm
176
Ena
j
Sc
i
Va
h
Cop
g
f
Ema
e
d
c
b
a
Pd
Gra
Gr
En
Pe
EE
1.0
Enc
Sc
Ena
Nut
Vas
Ema
Sc
Gra
Gr
i
Cop
Sc
Pe
h
Fl1
Ema
Adr
Cop
Pe
g
Epi
Adr
f
Col
Ema
a
Ema
b
Rt
Col
c
Pe
Rt
En
Ena
d
Rt
Gra
Nut
Pe
e

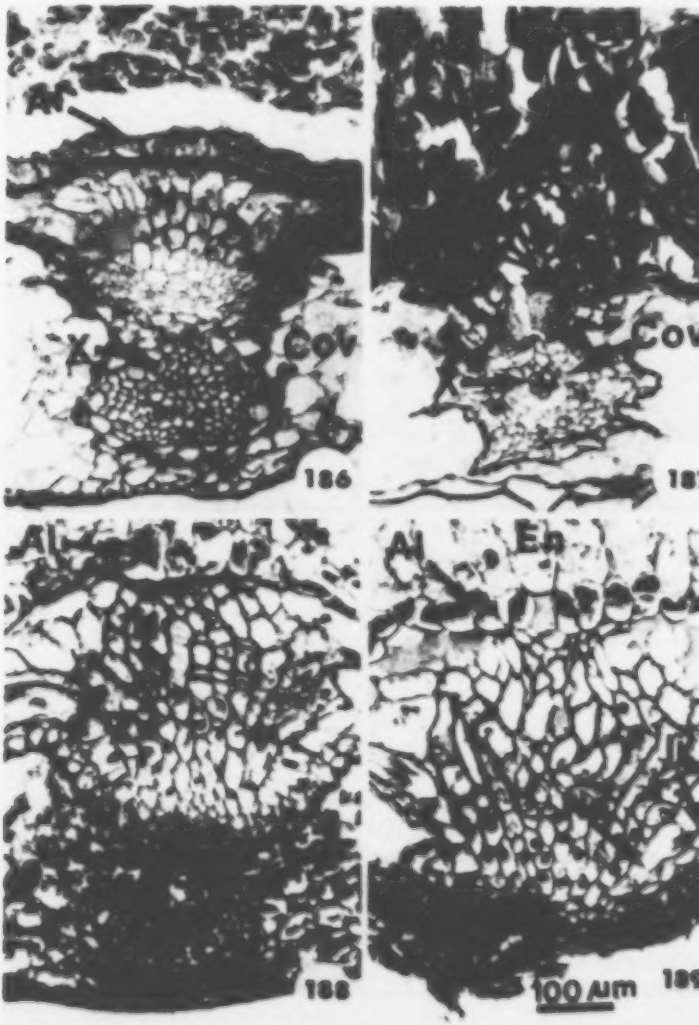
FIGURE 176

Structure and topography of tissues and organs in a mature caryopsis. Longitudinal or sagittal view of a caryopsis showing the position of embryo with reference to other tissues. Small alphabets (non-capitals) indicated by plain lines (no arrows) along the left side of the figure indicate approximately the levels at which sections were selected and studied. They correspond respectively to transverse sections diagrammed. (Adr, adaxial ridge; Al, aleurone layer; Col, coleorhiza; Cop, coleoptile; Ema, embryo aleurone layer; En, endosperm; Ena, endosperm aleurone layer; Enc, crushed endosperm; Epi, epiblast; Fl_1, first leaf (second cotyledon); Gr, groove; Gra, groove aleurone layer; Nut, nucellar tissue; Pd, pedicel; Pe, pericarp; Ps, pigment strand; Rt, primary root; Sc, scutellum (first cotyledon); Va, vasculature of scutellum (provascular tissue); Vas, vascular strand of carpel and ovule.) Magnification indicated by an arrow on the left-hand side top is only for that figure; scale in the middle is for other figures a-j.


177
178
Pd
179
Ft
Ra
180
181
182
Ra
183
184
185

FIGURES 177-185

Caryopsis and floret-enclosed caryopsis (includes floral parts, such as lemma, palea, lodicules and stamens) abscission. Fig. 177, Sagittal section of an ovary with an ovule at about the mature embryo sac stage showing a short pedicel, and the provascular tissue in it. The provascular tissue at the pedicel is surrounded by "spongy tissue" (arrow head). Fig. 178, Enlarged pedicel part to show the spongy tissue (arrow head). As there is still not much vascularization the pedicel may remain brittle. The ovary can abscise by slight mechanical pull. Fig. 179, The provascular tissue is well-developed and eventually a reasonable amount of xylem and phloem is differentiated, especially after fertilization in the embryo sac. Fig. 180, Sagittal section of a young spikelet to show the oblique abscission zone (arrow head) between the rachis and the first floret. Fig. 181, Enlarged view of the same abscission zone (arrow head) between the rachilla and the floret. Note the two vascular traces (bundles) and unevenly elongated parenchyma cells in the rachilla. There is more elongation of cells on the abaxial side of the rachilla than on its adaxial side. Fig. 182, A sagittal section at the region of abscission in a spikelet 15 days after anthesis. The cells in the base of the floret and those in the distal part of the rachilla become thick-walled. Abscission zone (arrow head) contains thin-walled cells. Note the vascular continuity between the floret and rachilla. Fig. 183, A tangential sagittal section showing abscission zone between the base of the lemma and the rachilla. Notice the difference in cell morphology between rachilla and base of lemma. On the abaxial side of the floret the cells in the base of lemma proliferate, often called callus. Fig. 184, In later stages of caryopsis development a continuous spongy tissue appears in the centre between the base of the floret and the rachilla below. There is no well-defined abscission zone in this region. In the periphery, however, it is observed (arrow head). Thick-walled cells in the periphery of rachilla become quite clear at this stage. Fig. 185, Longisection at the abscission zone showing two vascular traces of the rachilla extending into the floret, and these traces persist until the caryopsis is dislodged from the rachilla. (C, callus; Fb, floret bundle; Ft, floret; L, lemma; Pd, pedicel; Pv, provascular tissue; Ra, rachilla; Rb, rachilla bundle.) All figures same magnification.


Ar
X
Cov
186
Cov
Al
Al
En
188
100 µm

FIGURES 186-189

Development of pigment strand. Fig. 186, Cross section of caryopsis, 20 days after anthesis, the commissural vascular strand made up of ovular and carpellary vascular strands is still recognizable. Continuous xylem and phloem strands are present. Chalaza consists of nucellus often with thick-walled cells. Fig. 187, During further development of caryopsis, tissue obliteration commonly occurs on the adaxial side of caryopsis. Fig. 199, The cell walls of the chalazal nucellus thicken and the vascular tissue is highly compressed due to expansion of the seed (endosperm). Because also of the production of chemical degradatives, this entire composite tissue in this region appears pigmented brown, often referred to as pigment strand. Fig. 189, A mature seed shows persistent thick-walled chalazal nucellus (hypostase). The pericarp wall carrying the commissural bundle is also obliterated and compressed. (Al, aleurone; Cov, commissural or compound vascular strand; En, endosperm; Ii, inner integument; N, nucellus; Ne, nucellar epidermis, X, xylem.) All figures same magnification.

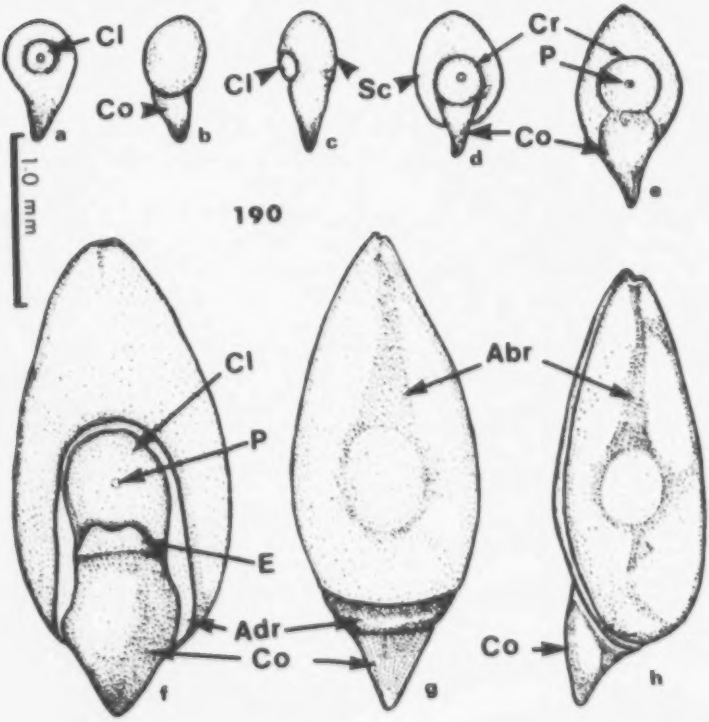

Cl
Co
a
b
Cl
Sc
c
d
Cr
P
Co
e
1.0 mm
190
Cl
P
E
Adr
Co
f
g
Abr
Co
h

FIGURE 190

Morphology and development of embryo. a, Young embryo isolated from a caryopsis, 7 days after anthesis, showing massive proembryonic tissue in which the coleoptile bud has broken through producing a scar (rim) around it on the adaxial side of young embryo. b, Abaxial view of the same showing the differentiation of proximal coleorhiza and distal scutellum. c, Sagittal side or view of the same with coleoptile bud, scutellum and coleorhiza parts in the young embryo. d, An older stage of embryo, 9 days after anthesis, with most embryo parts differentiated. e, Adaxial view of young embryo isolated from caryopsis, 11 days after anthesis, with well-developed coleoptile encloasingthe internal shoot apex; the coleorhiza is swollen enclosing the radicle primordium. The torn part of the proembryo (scutellum), through which coleoptile has protruded, forms the coleoptile rim which becomes the site of future adaxial ridge of the mature embryo. Part of the coleoptile rim situated proximal to the coleoptile bud becomes the site of epiblast origin. f, g, h, Mature embryo, 35 days after anthesis, showing embryo parts in different views, adaxial, abaxial and side views respectively. (Abr, abaxial ridge; Adr, adaxial ridge; Cl, coleoptile bud; Co, coleorhiza; Cr, coleoptile rime; E, epiblast; P, coleoptile pore; Sc, scutellum.) All figures same magnification.

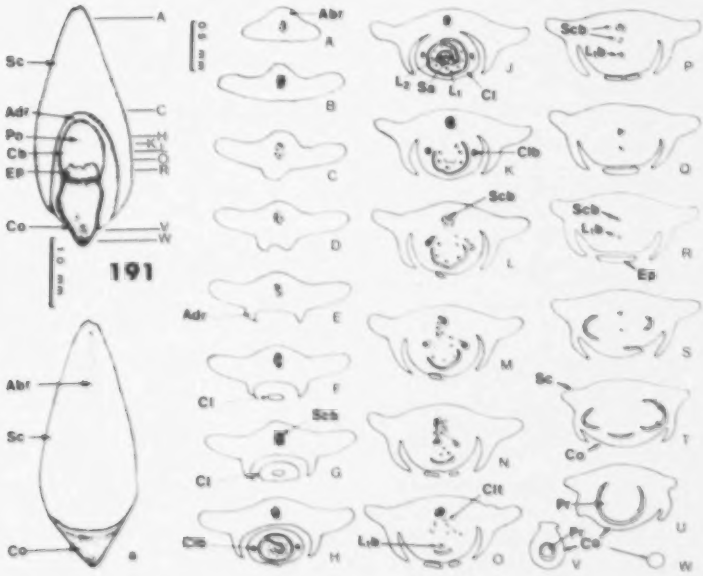
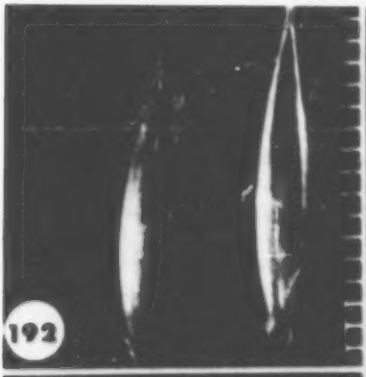
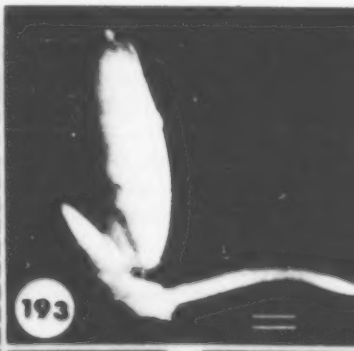

A
Sc
Adr
Po
Cb
Ep
Co
C
H
K
Q
R
V
W
191
Abr
Sc
Co
a
Abr
A
B
C
D
Adr
E
F
Cl
Scb
G
Cl
Clb
H
L2
Sa
L1
Cl
J
Clb
K
Scb
L
M
N
Clt
Lb
O
Scb
Lb
P
Q
Scb
Lb
Ep
R
S
Sc
Co
T
Pr
Co
U
V
W

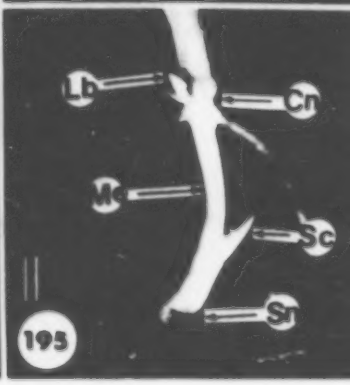
FIGURE 191

Anatomy of the mature embryo, isolated from an after-ripened caryopsis. The embryo contains mostly provasculature and a few isolated xylem and phloem elements in scutellum. Adaxial view of the embryo to show embryo parts which are indicated by bold-faced alphabets on the left. On the right, the capital alphabets (A, C, H, K, L, O, R, V, W) refer to levels of embryo sections selected and studied from serial sections diagrammed (A-W). a, Abaxial view of embryo to show a few visible embryo parts. (Abr, abaxial ridge; Adr, adaxial ridge; Cb, coleoptile bud; Cl, coleoptile; Clb, coleoptile bundle; Clt, coleoptile trace; Co, coleorhiza; Ep, epiblast; L_1, first leaf (second cotyledon); L_2, second leaf (first true leaf); L_1b, vascular bundle of first leaf; Po, coleoptile pore; Pr, primary root; Sa, shoot apex; Sc, scutellum; Scb, scutellar bundle.) Scale (1.0 mm) is for Figs. 191 and a; scale (0.5 mm) is for the rest.


192

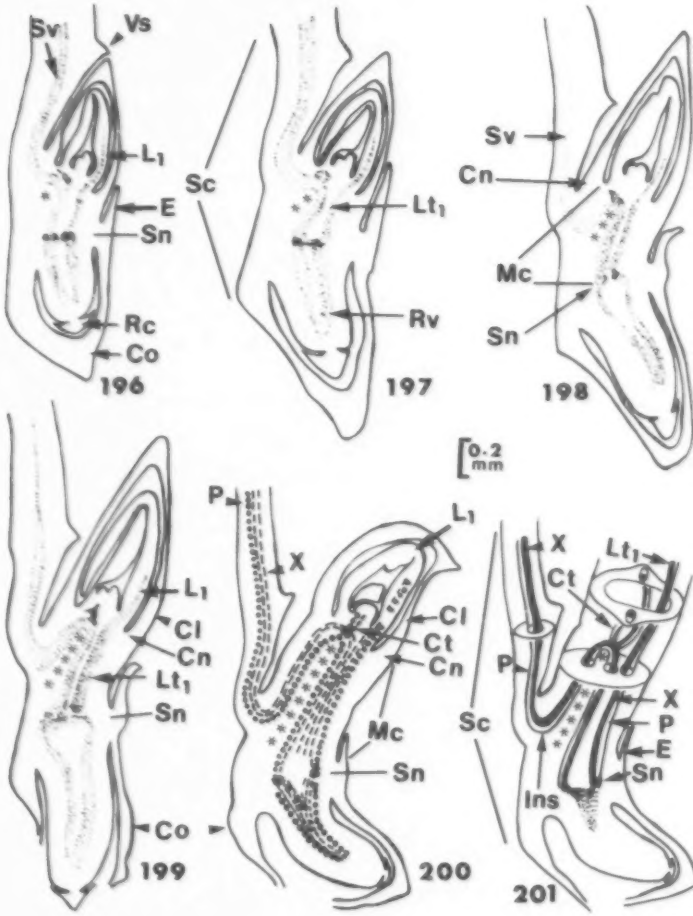

193

A
B
C
D
194
1.0 mm


Lb
Cr
Mc
Sc
Sr
195

FIGURES 192-195

Caryopsis and caryopsis germination. Fig. 192, Abaxial and adaxial views of mature caryopsis or floret-enclosed-caryopsis (CS 40 strain) of wild oats. Note the "sucker mouth" at the proximal end. Fig. 193, Germinated caryopsis with emerged shoot and root. Fig. 194, Embryos isolated from caryopsis during germination (A, embryo taken from ungerminated caryopsis. No growth in the scutellum, root or shoot. B, isolated embryo from a nondormant CS 40 germinated caryopsis. Growth is observed in the primary root and shoot. C and D, embryos from ungerminated dormant caryopses (An 51 strain) showing absence of root growth, but significant growth in the scutellum). Fig. 195, After caryopsis has germinated, and during early seedling growth the mesocotyl has elongated. Notice the bud in the axil of the first leaf (second cotyledon) at the coleoptile node. Scutellum in its axil also produces a bud conjoint with the coleoptile, and it does not usually develop, at least in the early stages. (Cn, coleoptile node; Lb, bud associated with the first leaf (second cotyledon); Me, mesocotyl; Sc, scutellum; Sn, scutellar node.) Scale in all figures 1.0 mm.


Sv
Vs
L1
E
Sn
Rc
Co
196
Sc
Lt1
Rv
197
Sv
Cn
Mc
Sn
198
0.2 mm
L1
Cl
Cn
Lt1
Sn
Co
199
P
X
L1
Cl
Ct
Cn
Mc
Sn
200
X
Lt1
Ct
P
Sc
X
P
E
Sn
Ins
201

FIGURES 196-201

Post seminal development of embryo. Camera lucida drawings of sections show the provasculature and vasculature of embryo in sagittal views. Fig. 196. A mature embryo before germination with the usual embryo parts. The scutellar (first cotyledon) provascular tissue extends proximally to the scutellar node. There is a small loop or indentation of the provasculature in the coleoptile node (asterisk). Note also the provascular strands of the first leaf (second cotyledon) also extending basipetally to scutellar node. Fig. 197. Embryo from a germinated caryopsis shows the elongation of the region between the scutellar node and the region of coleoptile attachment to the scutellum; the loop or indentation extends and becomes more conspicuous (two asterisks). Fig. 198. Embryo at a little later stage where the indentation has grown longer (three asterisks). Too keep up with the elongation of indentation the region on the abaxial side of embryo also elongates. The region between the coleoptile node and scutellar node elongates and it is considered as the hypocotyl or mesocotyl. Fig. 199. A little later stage of the embryo (young seedling) the indentation region has extended more (five asterisks). Fig. 200. Much older stage with the elongated (mesocotyl) region (eight asterisks) lifting up the coleoptile and the shoot apex. Due to elongation the outer scutellar trace becomes inverted. Fig. 201. Diagrammatic three-dimensional view of a young seedling to show scutellar and coleoptilar nodes, and the associated vascular bundles or traces in the indentation-region. Note also the termination of scutellar (first cotyledon) and first leaf (second cotyledon) traces proximally in the scutellar node. (Cl, coleoptile; Cn, coleoptile node; Co, coleorhiza; Ct, coleoptile trace or bundle; E, epiblast; Ins, inverted scutellar strand; L_1, first leaf (second cotyledon); Lt_1, first leaf trace; Mc, Mesocotyl; P, phloem; Rc, root cap; Sc, scutellum (first cotyledon); Sn, scutellar node; Sv, scutellar provascular tissue or strand; Vs, ventral or adaxial scale; X, xylem.) All figures same magnification.

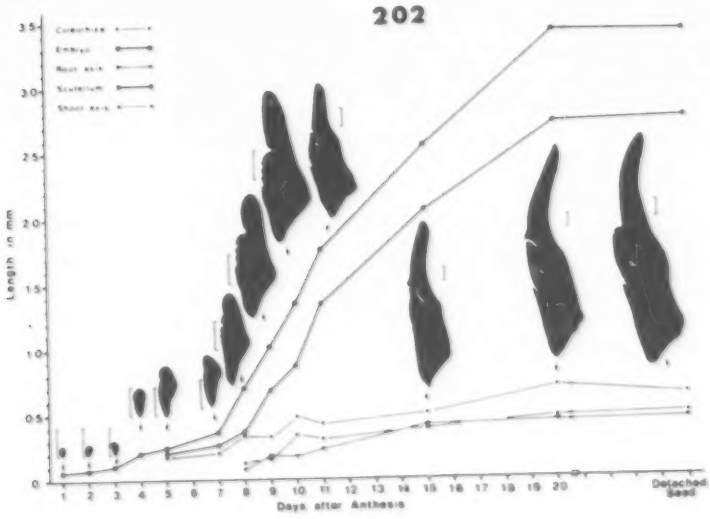

202
Length in mm
Days after Anthesis
Detached Seed

FIGURE 202

Growth of embryo and embryo parts after anthesis in wild oat caryopsis (CS 40 strain). The arrows emanating from ideogrammed embryos point at corresponding days after anthesis. Scale beside each embryo is 200 μm.

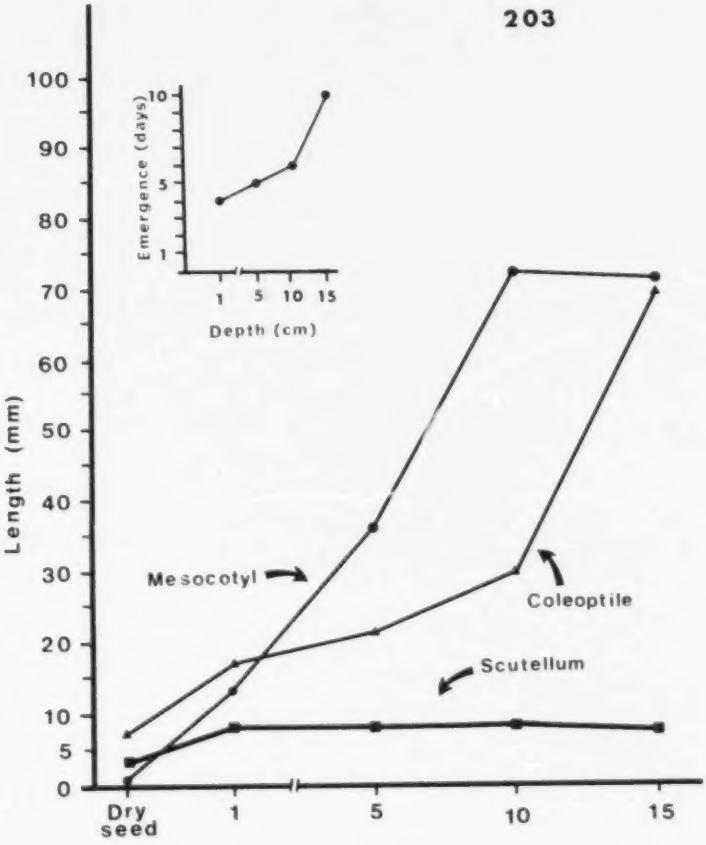

203
Length (mm)
100
90
80
70
60
50
40
30
20
10
5
0
Dry seed
1
5
10
15
Mesocotyl
Coleoptile
Scutellum
Emergence (days)
10
5
1
1
5
10
15
Depth (cm)

FIGURE 203

The graph indicates the effect of depth of seeding of wild oat caryopses (CS 40 strain) on emergence of seedlings (inset), and also the increase in length of some embryo parts.

TABLES

Table 1. Some morphological features of different varieties of wild oats (*Avena fatua* L.)* (N=20; sd, standard deviation)

Variety	Mean number of tiller/plant		Mean number of panicles/ plant		Mean number of nodes/ main panicle	
		(± sd)		(± sd)		(± sd)
MONTANA 73	9.70	2.29	9.15	1.63	6.90	0.64
IDAHO	9.05	1.50	6.65	1.73	6.65	0.75
AN 51	8.80	2.50	5.15	1.81	6.60	0.59
AN 474	9.20	2.17	5.80	1.82	7.20	0.62
SH 319	8.50	3.56	4.95	1.17	6.60	0.59
SH 430	7.55	1.67	5.95	1.43	6.55	0.69
CS 40	7.60	1.82	4.95	1.64	6.85	0.75

Variety	Mean number of nodes/ tiller panicle		Mean number of spikelets/ main panicle		Mean number of spikelets/ tiller panicle	
		(± sd)		(± sd)		(± sd)
MONTANA	7.00	0.65	41.50	7.40	32.45	6.14
IDAHO	6.75	0.55	38.80	7.90	31.95	6.37
AN 51	6.85	0.75	63.50	21.09	53.90	15.86
AN 474	5.80	0.69	70.10	11.43	63.20	12.89
SH 319	6.55	0.51	36.95	7.45	33.15	8.92
SH 430	6.60	0.68	35.65	6.96	33.35	8.86
CS 40	6.55	0.51	43.40	9.03	35.45	7.85

*Plants grown in the field

Table 2. Some measurements of floral parts of wild oats (*Avena fatua* L.)* (N =60; sd, standard deviation)

	AN 51 (dormant)				CS 40 (nondormant)			
	Primary caryopsis (mm)		Secondary caryopsis (mm)		Primary caryopsis (mm)		Secondary caryopsis (mm)	
		(± sd)		(± sd)		(± sd)		(± sd)
Lemma length	18.45	0.88	15.32	0.83	16.48	0.67	14.13	0.64
Rachis length	2.95	0.18	3.79	0.19	3.33	0.11	4.16	0.22

* From plants grown in the field

Table 3. Shape of suckermouth in wild-oat seeds (*Avena fatua* L.)* (N=100)

Variety	Caryopsis	Heart-Shaped	Oval-Oblong
AN 51	Primary	83	17
	Secondary	1	99
	Tertiary	98	2
CS 40	Primary	41	59
	Secondary	0	100
	Tertiary	61	39

*From plants grown in the field

Table 4. Homologies or concepts and functions of some wild-oat embryo parts

Embryo part	Homology	Probable Function
Scutellum	First cotyledon	Suctorial organ
Coleoptile	Part of scutellum Probably equivalent to lamina part of scutellum	Protection and keeps the shoot apex moist
First leaf	Second cotyledon	First photosynthetic leaf
Epiblast	No homology Adaxial extension (proximal) of coleorhiza	Taxonomic (?)
Coleorhiza	No homology	Protect primary root and probably helps in root emergence. Keeps the young primary root moist
Mesocotyl	Hypocotyl	Transitional region between shoot (epicotyl) and root. Helps in elevating epicotyl to ground surface from: greater depths after germination

Table 5. Some chronological events observed in the life cycle of *Avena fatua* L. (CS 40 strain) plants raised in growth cabinets. (The sequence of events listed below is comparable to the plants growing in the field.)

Events	Number of days from sowing
1. Dehulled floret-enclosed-caryopsis (caryopsis)	0
2. Caryopsis germinated	2-3
3. First leaf (not coleoptile) present	3
4. Second leaf present	5
5. Third leaf present	11
6. Short tillers appeared in axils of scutellum and first leaf. (Tiller in the axil of first leaf develops earlier)	15
7. Fourth leaf present. Change of vegetative shoot apex to floral apex (Fig. 3)	20
8. Fifth leaf present. Differentiation of young distal-most spikelet on the panicle (Fig. 4)	24
9. Sixth leaf present. Young spikelets at tips of branches of panicle are formed and the distal-most spikelet on the main axis is better differentiated (Figs. 6, 7)	26
10. Young spikelets differentiated on a branch in the lowermost node of the panicle (Fig. 8)	28
11. Seventh leaf present (flag leaf)	33
12. Panicle with differentiated spikelets before elongation of main axis (Figs. 11, 12)	38
13. Panicle emerged through the flag-leaf sheath (delayed by a week in dormant An 51 strain)	49
14. Florets on panicle begin to open (anthesis)	51
15. Complete emergence of panicle	61
16. Anthesis completed in the panicle	62
17. Yellowing of panicle at its distal end begins	63
18. Browning of flag leaf begins	78
19. Most mature seeds still attached to spikelets	93
20. Seeds (caryopses) begin to drop	98

Table 6. Some important chronological events during the development of caryopsis (seed) of *Avena fatua* L. (strain CS 40) plants raised in growth cabinets. (Sequence of events is approximately the same as that in plants in the field.) Events were recorded for first (primary) caryopsis only.

Events	Number of days from anthesis
1. Anthesis (floret opening): mature embryo sac in the ovule.	0
2. Fertilized egg or zygote appears with about 8-16 endosperm nuclei in the embryo sac.	1
3. A few-celled proembryo with many endosperm nuclei in the embryo sac appears.	2
4. Octant stage of the proembryo with large number of endosperm nuclei which become peripherally placed. Cell walls begin to form between endosperm nuclei.	4
5. Proembryo with more cells in it appears somewhat spindle-shaped. More endosperm cells appear.	5
6. Differentiation of embryo parts appears in the proembryo. Cells of endosperm are complete. Periclinal divisions on the abaxial part of endosperm begin.	6
7. Embryo is better differentiated, and most embryo parts are discernible. Starch grains begin to appear in endosperm cells, especially in the centrally placed cells.	7
8. Embryo differentiation is more advanced and embryo parts are quite clear. Divisions in the middle of endosperm cease. Divisions on the abaxial side of endosperm (periphery) begin. Aleurone cells begin to differntiate on the adaxial side of endosperm. More starch is added into endosperm cells.	8
9. Better developed embryo and endosperm. More starch in endosperm cells. Aleurone cells are differentiated around the embryo (on the adaxial side of embryo).	9
10. Embryo parts well-differentiated. Active divisions on the abaxial side of endosperm. Aleurone layer well-differentiated on the adaxial side. More starch synthesis in endosperm cells. Well-developed aleurone layer on the adaxial side of embryo.	10
11. All parts of embryo well-developed. Endosperm is still meristematic on the abaxial side. Adaxial aleurone cells well differentiated. More starch in endosperm cells.	11
12. Embryo parts present in the embryo. Meristematic activity is diminished on the abazial side of endosperm. Aleurone layer (embryo side) on the adaxial side of embryo is formed.	12
13. Same as 12. Caryopsis begins to lose water.	14-16
14. Caryopsis continues to lose water. Pigment strand on the axial side of caryopsis begins to appear.	17-18
15. Caryopsis is morphologically mature, and continues to dry. The aleurone layer on the abaxial side, including the cheeks, of the endosperm becomes distinct. Starch cells in endosperm begin to dry, and the grains become better visible. Pigment strand appears conspicuous.	20

The Wild Oat Inflorescence and Seed: Anatomy, Development and Morphology contains detailed information about the reproductive biology of the wild oat (*Avena fatua* L.), an annual persistent weed in the Canadian prairies and many other parts of the world. Essentially a description of the growth, structure, and development of the inflorescence (flowers) and the seed of the wild oat, the book also offers details relating to seed germination and post-seminal embryo development. The book is an important addition to the literature, as it includes some experimental results to strengthen the morphological interpretations of the reproductive parts, and to support the author's speculations relating to the onset and breakage of seed dormancy, and seed germination. Particular effort is made to provide information about the origin, structure, and development of embryo-coverings, and emphasis is placed on the role of embryo-coverings in seed dormancy, germination, and embryo growth.

Illustrated with more than 200 photographs and drawings, the book also includes lists of the chronology of events in the growth and reproduction of wild oat species which will be of considerable interest to biologists, botanical investigators, agronomists and agriculturists.

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